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METABOLISM OF L-HISTIDINE, CARNOSINE, AND ANSERINE IN SKIPJACK TUNA[1]

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The effects of some physiological conditions on the levels of L-histidine, carnosine, and anserine were examined in skipjack tuna, *Katsuwonus pelamis.* Also examined were the turnover rates of L-[U-^{14}C]histidine in skipjack blood and skeletal muscle, the metabolic interrelationship among several organs, and interconversion between histidine and the dipeptides. In white muscle of control tuna, these compounds in total occurred at a mean ± SD concentration of 147.4 ± 3.5 μmol/g muscle (n = 5) (histidine, 93.5 ± 9.2; carnosine, 2.90 ± 1.66; anserine, 51.1 ± 10.2 μmol/g muscle), but in red muscle the total concentration was only 21.3 ± 2.1 μmol/g muscle. Exhaustive burst swimming did not lead to any large changes in these concentrations, whereas starvation markedly affected them. In white muscle, histidine decreased to 30% and 4% of control levels after 5 and 12 days of starvation, respectively; carnosine increased 3.7- and 8.6-fold, while anserine decreased in the initial stage but recovered to control levels during sustained starvation. A similar pattern also was observed in red muscle. The metabolic half-life of ^{14}C-labeled histidine was 0.72 ± 0.124 h (n = 3) in skipjack blood, and 66 and 52.5 h in white and red muscle, respectively. The label was incorporated into muscle carnosine and anserine, though the incorporation was fairly slow. The label was transported rapidly from blood into liver and muscles and also from white muscle into red.

INTRODUCTION

Tuna are considered to be the "ultimate teleosts" (Hochachka 1980) in terms of their ability to reach high burst-swimming speeds (Waters and Fierstine 1964; Dizon, Brill, and Yuen 1978) and maintain muscle temperatures as much as 10 degrees C above ambient temperature (Stevens, Lam, and Kendall 1974). The tuna's ability to engage in burst swimming is sustained by elevated capacities for anaerobic glycolysis in the white muscle, typically represented by the activity of lactate dehydrogenase, which in tuna is the highest so far found in any animal (Guppy and Hochachka 1978). During burst swimming, large amounts of lactate, nearly 100 μmol/g muscle, are accumulated as an end product in white muscle (Guppy, Hulbert, and Hochachka 1979), accompanied by proton production (Hochachka and Mommsen 1983), which may have harmful effects. Not surprisingly, buffering capacity is typically high in tuna compared to other fishes (Castellini and Somero 1981).

Intracellular buffering capacity in vertebrate muscles is dominated by the imidazole group of L-histidine, which occurs (1) as histidine residues on protein, (2) as free L-histidine, and (3) as histidine-containing dipeptides, such as carnosine (β-alanyl-L-histidine), anserine (β-alanyl-N^{π}-methyl-L-histidine), and balenine or ophidine (β-alanyl-3-methyl-L-histidine). This free L-histidine and related dipeptides are widely distributed in vertebrate muscle (Crush 1970) at levels roughly proportional to anaerobic metabolic capacity (Hochachka and Somero 1984). Generally, most terrestrial mammals and amphibians contain large amounts of carnosine (2–20 μmol/g muscle). Aves and some fishes, in contrast, have higher levels of anserine than of carnosine in their muscle. Large amounts of balenine

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are found only in the muscle of snakes and whales (Crush 1970). One of these dipeptides, anserine, was reported to be synthesized from histidine via N^{π}-methyl-L-histidine (Harms and Winnick 1954) or via carnosine (McManus 1962). Among the scombrioids, species such as tuna and marlin are known to have large quantities of these compounds in their white muscle (Lukton and Olcott 1958; Suyama and Yoshizawa 1973; Abe 1981, 1983). A recently discovered clue to their physiological roles comes from studies of marlin white muscle, which contains 125 μmol/g muscle of histidine and related dipeptides (mainly anserine); this pool accounts for ~60% of total buffering capacity, whereas in trout white muscle a smaller pool (20 μmol/g muscle) constitutes only 25% of total buffering capacity (Abe et al. 1985). This indicates that at least one of the important physiological functions of these compounds is intracellular buffering of protons that are produced during burst swimming, though other possible roles have been proposed; for example, when copper complexed, they may serve as oxygen transporters for cytochrome oxidase (Brown 1981) or as direct activators for some enzymes (Parker and Ring 1970).

Despite this interesting background on these compounds, there is literally no information on the metabolism of histidine and related dipeptides in tuna or marlin. For this reason, we decided to investigate the turnover patterns of L-histidine in tuna muscle and blood, the interrelationship of histidine metabolism and exchange in different tissues and organs, and the potential interconversions between histidine and related dipeptides.

MATERIAL AND METHODS

Live skipjack tuna, *Katsuwonus pelamis* (wt 1,130–2,130 g), and kawakawa, *Euthynnus affinis* (wt 750–1,180 g), captured on hook and line were obtained from local fishermen at Kewalo Basin, Honolulu, Hawaii. They were kept in large holding tanks supplied with aerated seawater (25 C) at Kewalo Research Facility of the National Marine Fisheries Service's Honolulu Laboratory. Kawakawa used in these studies were well fed on frozen smelt daily. Unless noted otherwise, skipjack tuna were not fed and were used within 5 days of capture. Control tuna were hooked at sea on a commercial fishing vessel and had muscle samples excised immediately after capture. Exhausted fish were those sampled after burst swimming in the holding tank.

L-[U-^{14}C]histidine (348 mCi/mmol; radioactive purity 95.5%) was purchased from Amersham Corporation, Oakville, Ontario. It was dried under N_2 and brought to 40 μCi/ml with physiological saline containing 40 μmol/ml L-histidine. Other reagents were obtained from Sigma Chemical Company, St. Louis, Mo.

CANNULATION

Skipjack tuna were anesthetized with tricaine methane-sulfonate (1:15,000) and maintained by perfusing aerated seawater (22–24 C) containing the anesthetic (1:30,000) over the gills. A cannula was implanted into the ventral aorta just anterior to the heart, a procedure taking approximately 5–10 min. Cannulated fish were kept lightly anesthetized during experimentation (3–6 h). Anesthetic and surgical procedures were as described by Jones, Brill, and Mense (1985).

ADMINISTRATION OF THE TRACER

The cannulated tuna received 30 μCi of L-[U-^{14}C]histidine via the cannula, followed by several volumes of saline wash. Serial blood samples (0.5 ml each) were withdrawn at appropriate time intervals for assessing the decay in specific activity of histidine.

A second group of fish received 30 μCi of labeled histidine intramuscularly 1 day after capture and were kept in a holding tank. At appropriate time intervals muscle samples were excised from freshly killed fish.

EXTRACTION OF L-HISTIDINE AND RELATED COMPOUNDS

Blood samples were mixed with an equal volume of 10% trichloroacetic acid and centrifuged. The supernatant was kept at −20 C and used for the determination of total radioactivity and for the fractionation of histidine-related compounds by high-performance liquid chromatography (HPLC).

Muscle samples (1 g) were homogenized in 5 ml of 1% picric acid with a Polytron homogenizer (Kinematica, Zurich, Switzerland). The homogenate was centrifuged, and the pellet was rehomogenized in 5 ml of the acid. Both supernatants were combined and applied to a column (0.5 × 1.5 cm) of Dowex 2 × 8 (200–400 mesh, Cl^- form). The eluate and washings obtained with 0.01 N HCl were freeze-dried and brought to a volume of 1 ml with distilled water.

DETERMINATION OF L-HISTIDINE AND RELATED COMPOUNDS

L-Histidine and its related compounds were determined by HPLC essentially as described previously (Abe 1981). A Spectra Physics SP-8000B liquid chromatograph equipped with Zipax SCX column (0.21 × 50 cm; Shimadzu, Japan) was used. Elution was carried out under isocratic conditions for 10 min using 12 mM KH_2PO_4 at 35 C and a flow rate of 1 ml/min followed by a gradient up to 30 mM. UV detection was used at 210 nm with 0.04 absorbance units at full scale.

For the determination of specific radioactivity, the concentrated extract was injected into the HPLC column and a 2-ml fraction of the eluate was collected. The L-histidine, carnosine, and anserine fractions were evaporated to dryness in vacuo and dissolved into HPLC-grade water.

DETERMINATION OF RADIOACTIVITY

A Beckman LS 9000 liquid scintillation counter was used (1) on the blood and tissue extracts (10–500 μl) to determine total radioactivity and (2) on combined fractions (1 ml) obtained from the HPLC column to determine specific radioactivity of histidine, carnosine, and anserine fractions. As a scintillant, 10 ml of ACS II (Amersham, Oakville, Ontario) was used with plastic scintillation vials obtained from Canlab, Vancouver, B.C. Counting efficiency was >90%, and the background fell between 30 and 50 dpm.

In all cases statistical analyses were performed using Student's *t*-test—or the Cochran-Cox test when the variances were different.

RESULTS

EFFECT OF PHYSIOLOGICAL CONDITIONS ON L-HISTIDINE AND DIPEPTIDES IN TUNA

Control tuna showed extremely large amounts of L-histidine and anserine and lesser amounts of carnosine in their white muscle (table 1). Although some of these values closely coincided with those previously reported for different populations (Abe 1983), anserine content was much higher in the Hawaiian samples. The concentrations of histidine compounds in red muscle (table 1) were lower than those in white muscle, the total content being only one-seventh that observed in white muscle (table 1). This is a typical distribution pattern of these compounds in fish muscle that contains them in large amounts (Abe 1983; Abe et al. 1985). Red muscle, in addition, contained small but detectable amounts of N^{π}-methyl-L-histidine, whereas white muscle did not. Individual differences in the concentration of each compound were rather large, but the combined total pool size in white muscle was similar among individuals. This was also the case with red muscle (table 1).

In white muscle of exhausted fish, anserine concentration was not different from that in controls. Histidine, on the other hand, increased significantly ($P < .05$). However, we found no significant changes in these compounds in red muscle following burst swimming. The increase of total histidine-related compounds, equivalent to ~20 μmol/g muscle in white muscle ($P < .001$) was due entirely to histidine increases.

Starvation of skipjack tuna also resulted in changes in the concentrations of these compounds (table 2). Although we found rather large individual differences in each compound, on average, histidine levels in white muscle decreased significantly ($P < .01$) from those in controls. Carnosine, on the other hand, showed a marked increase ($P < .01$), whereas anserine showed no large changes. Tunas 7 and 8, which were starved for 5 and 12 days after capture, respectively, showed an extremely large decrease in histidine and an increase in carnosine. Anserine concentrations were practically identical to those in the controls.

TABLE 1

CONCENTRATION (µmol/g muscle) OF L-HISTIDINE AND RELATED COMPOUNDS IN WHITE AND RED MUSCLE OF SKIPJACK TUNA

GROUP AND NO.	WHITE MUSCLE				RED MUSCLE				
	His	Car	Ans	Total	His	N^{π}-meHis	Car	Ans	Total
Control Fish:									
1	99.5	.672	49.2	149.4	14.0	.212	.212	7.36	21.8
2	84.2	5.00	52.7	141.9	12.6	.232	.917	7.66	21.4
3	98.5	4.50	46.1	149.1	13.3	.050	.883	6.90	21.1
4	104.2	2.74	38.2	145.1	11.7	.227	.512	5.32	17.8
5	81.0	1.57	69.1	151.7	14.7	.184	.256	9.29	24.4
Mean ± SD	93.5 ± 9.2	2.90 ± 1.66	51.1 ± 10.2	147.4 ± 3.5	13.3 ± 1.1	.181 ± .068	.556 ± .299	7.31 ± 1.28	21.3 ± 2.1
Exhausted Fish:									
1	111.8	12.7	40.7	165.2	17.2	.039	1.97	7.08	26.3
2	104.4	6.69	50.7	161.8	14.3	.041	.644	7.41	22.4
3	133.9	3.25	29.6	166.8	26.1	.046	.988	9.99	37.1
4	119.3	4.49	47.2	171.0	13.9	.172	.941	8.78	23.8
Mean ± SD	117.4 ± 10.9*	6.78 ± 3.63	42.1 ± 8.03	166.2 ± 3.3**	17.9 ± 4.9	.075 ± .056	1.14 ± .50	8.32 ± 1.16	27.4 ± 5.8

NOTE.—Control fish were obtained on a commercial fishing boat just after capture. Exhausted fish are those kept in a tank on the boat, transported to the harbor, and killed or dead after burst swimming in the holding tank. His = L-histidine; Car = carnosine; Ans = anserine; N^{π}-meHis = N^{π}-methyl-L-histidine.

* $P < .05$.

** $P < .001$.

TABLE 2

EFFECT OF STARVATION ON THE LEVELS (μmol/g muscle) OF L-HISTIDINE AND RELATED COMPOUNDS IN WHITE AND RED MUSCLE OF SKIPJACK TUNA

		WHITE MUSCLE				RED MUSCLE				
TUNA NO.	DAYS AFTER CAPTURE	His	Car	Ans	Total	His	N$^{\pi}$-meHis	Car	Ans	Total
1	1	79.9	14.7	19.1	113.7	1.05	+	.439	.580	2.07
2	1	87.8	5.89	40.6	134.3	6.59	.020	.994	5.51	13.1
3	2	74.1	4.94	47.8	126.8	8.67	.101	.713	9.12	18.6
4	2	69.1	12.1	34.3	115.5	10.9	.069	2.66	7.91	21.5
5	2	40.3	7.70	38.3	86.3	7.21	.292	1.57	8.90	18.0
6	3	65.3	13.9	36.5	115.7	9.71	.075	3.04	9.00	21.8
7	5	31.5	10.6	64.0	106.1	3.92	.550	1.96	9.78	16.2
8	12	3.46	24.9	58.8	87.2	3.59	.118	4.86	13.3	21.9
Mean ± SD		56.4 ± 26.9*	11.8 ± 5.9*	42.4 ± 13.4	110.7 ± 16.0**	6.46 ± 3.16**	.153 ± .171	2.03 ± 1.37*	8.01 ± 3.46	16.7 ± 6.2

* $P < .01$.
** $P < .001$.

TABLE 3

CONCENTRATION (μmol/g muscle) OF L-HISTIDINE AND RELATED COMPOUNDS IN WHITE AND RED MUSCLE OF KAWAKAWA *Euthynnus affinis*

	WHITE MUSCLE				RED MUSCLE				
GROUP AND NO.	His	Car	Ans	Total	His	N^{π}-meHis	Car	Ans	Total
Captivity control:									
1	68.7	1.30	32.5	102.5	6.97	.037	.772	4.26	12.0
2	74.3	1.19	27.7	103.6	5.43	.054	.198	5.20	10.9
3	83.3	.780	22.8	106.9	7.14	.025	.084	3.98	11.2
Mean ± SD	76.5 ± 5.99	1.09 ± .22	27.7 ± 3.96	104.3 ± 1.87	6.51 ± .77	.039 ± .012	.351 ± .301	4.48 ± .52	11.4 ± .46
Starved fish (days):									
1 (6)	50.0	.439	22.1	72.5	4.61	.008	.068	8.25	12.9
2 (6)	73.4	2.1	33.2	108.7	15.4	.038	.297	7.13	22.9
3 (9)	65.0	.390	49.0	114.4	6.99	.303	.298	18.0	25.6
4 (13)	48.4	.372	52.8	101.6	10.0	.224	.150	15.2	25.6
5 (15)	78.1	.231	35.5	113.8	7.98	.269	.141	15.4	23.8
6 (18)	35.7	2.26	38.5	76.5	4.01	.299	.441	12.1	16.9
Mean ± SD	58.4 ± 15.0	.965 ± .863	38.5 ± 10.2	97.9 ± 17.1	8.17 ± 3.81	.191 ± .122*	.233 ± .125	12.7 ± 3.93**	21.3 ± 4.76**

NOTE.—Captivity controls are those well fed in captivity.
* $P < .05$.
** $P < .01$.

Generally during starvation, histidine appeared to decline rather markedly, with part of it probably being converted into carnosine. Anserine, however, decreased during the initial stage of starvation, but later it recovered to normal levels, probably by the conversion from histidine. As a result, the total content of these compounds per gram of white muscle decreased significantly ($P < .001$), but the decrease was not as large as the fall in histidine levels. This pattern of a significant decrease in [histidine] ($P < .001$), an increase in [carnosine] ($P < .01$), and small fluctuations in [anserine] during starvation was also observed in red muscle.

Kawakawa, a species closely related to skipjack tuna, showed similar results, though the degree of change with starvation was less (table 3). The total levels of these histidine-related compounds in well-fed, captive fish were almost 30% and 50% lower ($P < .001$) than those in skipjack white and red muscle, respectively. The composition of these compounds, however, was almost the same as in skipjack tuna, showing high histidine, high anserine (almost half the level of histidine), and low carnosine concentrations.

The levels of these compounds in blood of both skipjack and kawakawa were low, and we found no differences between these two species (table 4). It was a rather characteristic feature of the blood, however, that the level of carnosine exceeded that of anserine. Blood carnosine levels were almost identical to, or a little higher than, those in red muscle.

TURNOVER OF L-[U-^{14}C]HISTIDINE IN SKIPJACK TUNA

Three cannulated skipjack tuna received 30 µCi of L-[U-^{14}C]histidine, and decay curves were obtained for total and specific radioactivities of L-histidine (figs. 1, 2). The three specimens showed very little individual difference, as shown by the small standard deviation. Specific radioactivity of histidine was calculated (fig. 2) as dpm/µmol of histidine. To judge from such curves, the decay of histidine specific activity and the incorporation into tissues were considered to be rapid. Histidine replacement rate in the blood was calculated (according to Katz et al. 1974) as 2.60 ± 0.65 µmol/100 g body weight h^{-1} and metabolic half-life as 0.72 ± 0.124 h. This replacement rate is similar to that in rainbow trout (H. Abe and P. W. Hochachka, unpublished data). Corrected to the same temperature (assuming a Q_{10} of 2), the replacement rate is actually slower in tuna than in trout (the water temperatures for the two species were 24 and 6 C, respectively). This difference was also evident in the metabolic half-life, which was 0.72 h in tuna but 1.99 h in trout (H. Abe and P. W. Hochachka, unpublished data).

METABOLISM OF L-HISTIDINE IN TUNA TISSUES

After blood sampling was completed (5.5 h), the tuna were killed, and white muscle, red muscle, and a liver and final blood sample were obtained. In these tissues, the total activity and the specific activities of histidine, carnosine, and anserine were determined (table 5). We found only small

TABLE 4

CONCENTRATION (µmol/g blood) OF L-HISTIDINE AND RELATED COMPOUNDS IN THE BLOOD OF SKIPJACK TUNA AND KAWAKAWA

Fish Type and No.	Histidine	Carnosine	Anserine	Total
Skipjack tuna:				
1	2.11	.852	.074	3.04
2	1.84	.889	.023	2.75
3	.783	.440	.054	1.28
4	.843	.618	.027	1.49
5	1.55	.555	.024	2.13
Mean ± SD	1.43 ± .53	.671 ± .173	.040 ± .020	2.14 ± .69
Kawakawa	.806	.868	.049	1.72

NOTE.—Whole blood was used for the analysis after deproteinization with trichloroacetic acid.

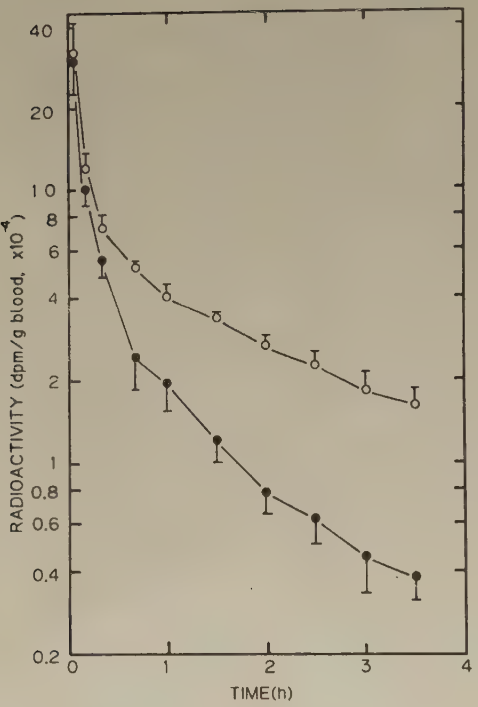

FIG. 1.—Total and specific radioactivity in the blood of skipjack tuna. A bolus of L-[U-^{14}C]histidine (30 μCi/tuna) was injected into the aorta through a cannula. ○——○ = Total radioactivity; ●——● = specific radioactivity of L-histidine. Blood samples were withdrawn ≥2 min after injection via cannula under the shallow anesthetic condition. The mean and standard deviation for three tuna are shown in dpm/g blood.

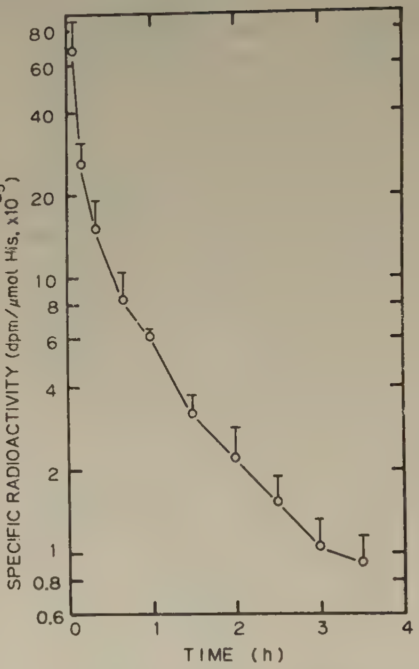

FIG. 2.—Specific radioactivity of L-histidine in the blood of skipjack tuna. The activities are shown in dpm/μmol of histidine for the same samples as those in fig. 1.

amounts of labeled histidine being incorporated into carnosine and anserine. Per gram of tissue, red muscle contained a much larger amount of total activity than did white muscle. The total of specific activities of these compounds in liver was equivalent to only 7.3% of total radioactivity in the liver, indicating a rapid catabolism of amino acids in this organ. In blood, only 36% of the radioactivity was in carnosine, anserine, or histidine, whereas in white and red muscle the values were 103% and 90%, respectively. These data suggest that only modest catabolism of histidine occurs in the muscle.

In addition to the 5.5-h sample, the incorporation of the label into tissues was also examined in tuna sampled at several shorter time intervals (fig. 3). The incorporation

TABLE 5

TOTAL RADIOACTIVITY AND SPECIFIC RADIOACTIVITY OF L-HISTIDINE, CARNOSINE, AND ANSERINE IN SEVERAL TISSUES OF SKIPJACK TUNA

	RADIOACTIVITY (dpm/g tissue, ×10^{-3})			
TISSUE	Total Activity	Histidine	Carnosine	Anserine
White muscle	8.02	7.16	.250	.815
Red muscle	35.6	31.5	.160	.436
Liver	51.9	2.51	.718	.562
Blood	8.64	2.54	.342	.233

NOTE.—Tissues were collected 5.5 h after L-[U-^{14}C]histidine injection (30 μCi/tuna) into the aorta.

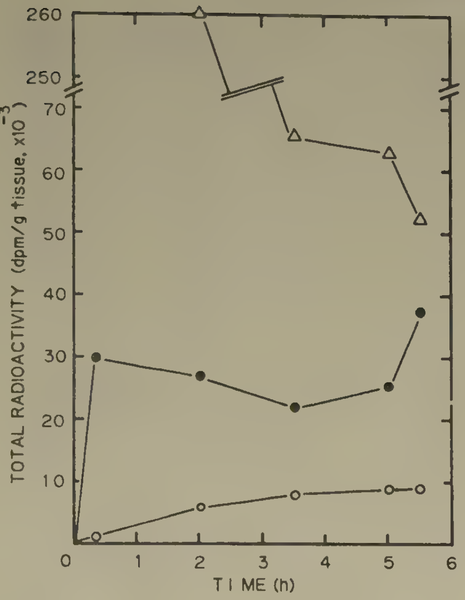

FIG. 3.—Incorporation of total radioactivity into white and red muscle and liver after bolus injection of L-[U-^{14}C]histidine (30 μCi/tuna) into the aorta. Tissue samples at 3.5, 5.0, and 5.5 h were obtained from the tuna shown in fig. 1. ○——○ = White muscle; ●——● = red muscle; △——△ = liver. Each point represents one tuna sample.

into the liver was extremely high compared to that in skeletal muscle. The radioactivity taken up into red muscle was always higher than that taken up into white muscle.

In free-swimming fish, if the label was administered into white muscle, the decay of the radioactivity from the muscle was slow, whereas the label was taken up by red muscle promptly after injection (fig. 4). The decay curve was sharper for red than for white muscle. From these curves, the metabolic half-lives of histidine in white and red muscle were calculated as being 66 h and 52.5 h, respectively. During these studies, the label was apparently incorporated into anserine (fig. 5) both in white and in red muscle. This incorporation was much higher in white than in red muscle.

DISCUSSION

Several scombrioids (suborder; Scombrioidei) are known to contain extraordinarily large amounts of histidine and histidine-related dipeptides in their white muscle; for instance, some scombrids (mackerel and tuna) contain 30–100 μmol/g of histidine and 10–50 μmol/g of anserine (Lukton and Olcott 1958; Suyama and Yoshizawa 1973; Abe 1983). Some istiophorids (marlin) contain 16–54 μmol/g of histidine and 15–120 μmol/g of anserine (Suyama and Yoshizawa 1973; Abe et al. 1985). Of these fishes, skipjack tuna shows the highest histidine content (table 1), whereas Pacific blue marlin (*Makaira nigricans*) shows the highest anserine concentration (90–120 μmol/g muscle; Abe et al. 1985) of all vertebrates thus far examined. These species all belong to a fast-

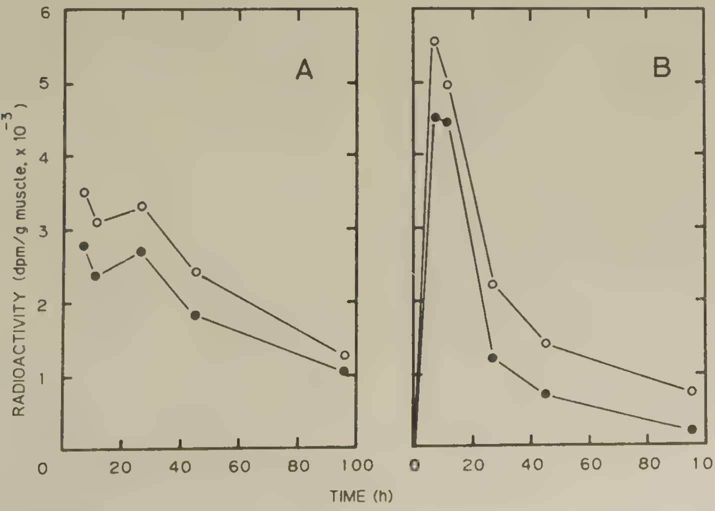

FIG. 4.—Total and specific radioactivities in white and red muscle of skipjack tuna after injection of L-[U-^{14}C]histidine (30 μCi/tuna) into white muscle. Each point represents one skipjack tuna. *A*, White muscle, *B*, red muscle. ○——○ = Total activity; ●——● = specific radioactivity of L-histidine.

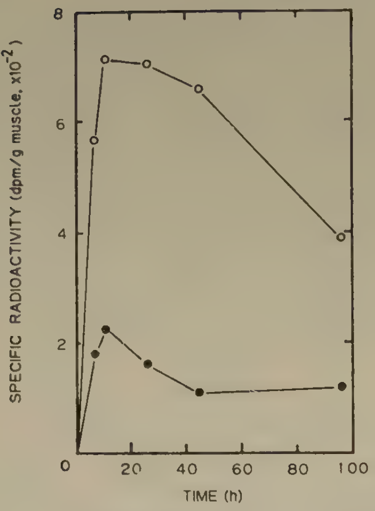

FIG. 5.—Incorporation of the label into anserine in white and red muscle of tuna after intramuscular injection of 30 μCi of L-[U-^{14}C]histidine into white muscle. The same muscle samples as shown in fig. 4 were used for anserine-specific radioactivity. ○——○ = White muscle; ●——● = red muscle.

swimming group of fishes that have adapted both for endurance and for burst anaerobic exercise. Red muscle of these fishes shows much lower contents of these compounds than does white muscle, which is consistent with these compounds playing a proton-buffering role correlated with anaerobic metabolism. Our control fish, captured at sea, are considered to have been sampled during high-speed, steady-state swimming associated with feeding; thus, in such high-activity states, tuna apparently maintain high total contents of these compounds, although there are some individual differences in how each compound contributes to the total pool.

In tuna exhausted after burst swimming, the histidine content of white muscle increases by an average of 20 μmol/g. Since histidine is considered nutritionally to be an essential amino acid in all fish species thus far examined, this increase in histidine concentration may be derived from the degradation of body proteins or from dietary proteins eaten just before capture. These data therefore are equivocal and may not mean that an interconversion between these compounds necessarily occurs during burst swimming.

Starvation, on the other hand, markedly affects the composition of this pool of histidine-related compounds (table 2). In the initial stage of starvation, both histidine and anserine levels decrease with a concomitant rise in carnosine concentration. The decline in histidine concentration may mean that this amino acid is utilized as an energy source via the Krebs cycle or as a glucose source via the Cori cycle during starvation. If used as an energy source directly, a mole of histidine oxidation could yield 21 mol of adenosine triphosphate. Although this metabolic fate is possible in principle, in practice it does not seem to occur. Instead, during sustained starvation the decomposition of anserine is arrested, whereas free L-histidine appears to be converted into carnosine and anserine, suggesting that the biosynthetic pathway of anserine in tuna may be via carnosine, as occurs in trout (H. Abe and P. W. Hochachka, unpublished data).

This interconversion may have an important implication, namely, that white muscle "defends" the total pool size of these compounds in order to maintain its proton-buffering capacity. This is also supported by the fact that the total concentration of these compounds was rather similar among individuals, though a rather large difference was found in the level of each compound (table 1). As a result of this arrangement, even if histidine is depleted almost completely during starvation, the total pool size of these compounds decreases by only 30%–40%. This is also true for red muscle. These effects of starvation are also supported by the results obtained from the starvation of

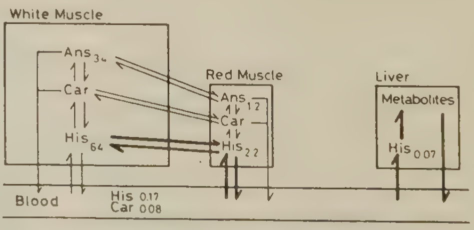

FIG. 6.—Proposed interrelationship of the metabolism of L-histidine and related dipeptides among several tissues and organs of skipjack tuna. Values indicated are total amounts of L-histidine and anserine in the tissue (mmol/tissue). The heavy lines show the main and fast processes.

kawakawa (table 3), though the changes observed in the latter were smaller.

A common metabolic response to starvation among tuna thus appears to be the defense of the total pool size of histidine-related compounds. This implies that the physiological reason for large accumulations of free L-histidine specifically in tuna white muscle is the same as that obtaining for large accumulations of the related dipeptides: in effect, histidine is an intracellular buffer, equivalent mole for mole, with either dipeptide. Its disadvantage is that it is more metabolically reactive. That is presumably why the conversion of histidine into much more metabolically inert forms (i.e., carnosine and anserine) is necessary. In this view, these dipeptides are a "histidine sink" that can keep the total histidine-related buffering capacity at high values. This end is not so easily achievable with histidine per se because it can be utilized easily in the other metabolic pathways according to the physiological conditions. Our data and interpretations are in agreement with studies on starved eels, trout, and Japanese dace, which show no decrease of the dipeptide pool but a notable decrease in histidine levels during long-term starvation (H. Abe, unpublished data). Similarly, during spontaneous starvation accompanying upstream spawning migration in the sockeye salmon, histidine decreases to about one-tenth normal levels, whereas anserine levels remain unchanged (Mommsen, French, and Hochachka 1980).

The turnover of L-histidine in skipjack tuna blood is rapid, and almost the same as that in trout blood (H. Abe and P. W. Hochachka, unpublished data); however, it is much slower when comparisons are corrected for temperature differences. In white muscle, the metabolic half-life of L-histidine is 66 h, which implies much faster turnover in tuna than in trout muscle (half-life of 7.5 days). However, this difference disappears if one makes a simple Q_{10} correction of ~2, in which case the half-life of histidine in tuna white muscle would be 11 days at 4 C. However, since skipjack tuna maintain muscle temperatures significantly above ambient temperatures, this fast turnover in white muscle suggests that histidine metabolism is probably quite rapid under the normal conditions of this species at sea. To put this in perspective, it should be noted that the metabolic half-life of L-histidine in rat gastrocnemius muscle is ~3.6 h (Tamaki et al. 1980); so the above data indicate a rather slow absolute turnover rate for this amino acid in tuna muscle.

Although some conversion of histidine into carnosine and anserine occurs following injection of histidine into the ventral aorta (table 5), following intramuscular injection the label is also incorporated into anserine, especially in white muscle (fig. 5). The appearance of only a small amount of the label in anserine is taken to indicate that the rate of anserine biosynthesis is slow in skipjack as it is in trout (H. Abe and P. W. Hochachka, unpublished data), possibly because of limited β-alanine availability. In white muscle, β-alanine occurred at 0.016 ± 0.005 μmol/g in the control tuna (n = 5) and at 0.054 ± 0.0115 μmol/g in red muscle. These values are lower than those in trout white muscle, where β-alanine's availability seems to determine rates of dipeptide synthesis (H. Abe and P. W. Hochachka, unpublished data). Thus it is reasonable to conclude that the level of β-alanine also may be a factor controlling the rates of biosyntheses of these dipeptides in tuna muscle.

The uptake of the label from blood into red muscle was much faster than that from blood into white muscle (fig. 3), and the label was also transferred efficiently into red muscle from white muscle in which it was initially administered (fig. 4). These data are consistent with a direct transfer of L-histidine from white to red muscle, possibly via exchange at the rete (as suggested for lactate movement during recovery from exercise [P. W. Hochachka, unpublished data]). Red muscle, with its high capillary density, is then the main site for equilibrating muscle and blood pools of histidine.

According to the above considerations, although exact rates and pathways are not known, the main movements of L-histidine and related compounds in skipjack tuna may be summarized as shown in figure 6. The incorporation and decomposition of L-histidine by liver (possibly also by kidney) are very fast, indicating that most of the histidine derived from dietary proteins is used as a carbon and energy source in the liver. However, there occurs a constant incorporation and accumulation of the amino acid into white muscle, and the biosyntheses and degradations of carnosine and anserine appear to proceed both in white and in red muscles. Both L-histidine and anserine are accumulated in white muscle, the former being slowly metabolized to the latter in muscle in order to stabilize a large pool of imidazole-based intracellular buffering capacity even under conditions of starvation.

These conclusions raise interesting problems about the turnover of carnosine and anserine in white muscle; about why anserine, not carnosine or balenine, has been selected by this species; and about interorgan transfer and metabolism of these metabolites.

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FATAL SHARK ATTACK ON A HAWAIIAN MONK SEAL (*MONACHUS SCHAUINSLANDI*)

We describe here a fatal attack on a Hawaiian monk seal, *Monachus schauinslandi,* apparently initiated by tiger sharks, *Galeocerdo cuvier.* The attack occurred near sunset at 1957 h on 28 May 1982, 15 m off the landing beach on the west side of Laysan Island (25°42′N, 171°44′W), Northwestern Hawaiian Islands. Observations were made from shore at a distance of approximately 33 m.

Predation by sharks on this endangered species is indicated by the presence of monk seal remains in tiger sharks (Taylor and Naftel 1978), tiger sharks seen feeding on dead seals (Balazs and Whittow 1979, Johanos and Kam 1986), a tiger shark seen injuring a seal (Johanos, unpubl. ms.) and apparent shark-inflicted wounds on monk seals (*e.g.,* Wirtz 1968, Kenyon 1973, Johnson and Johnson 1978, Alcorn 1984), but a fatal attack on a live monk seal has not been documented.

First attack—At 1929 h the fins of a large tiger shark were seen about 12 m offshore, near two monk seals. One seal, an adult, appeared by its behavior to be a male; the other seal was the size of a subadult with open pink puncture wounds on its back and sides and shallow tears as long as 8 cm. The wounds were not bleeding and were at least a few days old; we had seen them on this seal 3 d earlier. At that time, the subadult was tentatively identified as a female, based on behavioral responses to an approaching adult male. The wounds were not caused by a shark but were the type inflicted by adult male seals during mating attempts (Johnson and Johnson 1978, E. Shallenberger pers. comm.). Such injuries occur most frequently on adult and subadult females and at geographic locations where adult male seals outnumber adult females.

The subadult rested on the surface and the adult circled it as the two seals drifted towards shore. They were within 6 m of shore when two large sharks approached from the south. The sharks were submerged but visible in the clear, shallow water. One veered seaward when about 30 m from the seals, and the other shark continued to approach at moderate speed. The approaching shark was twice the length of the approximately 2.1 m long adult seal. When the submerged shark had almost reached the seals, the adult ceased circling and rapidly swam between the injured subadult and approaching shark. The three shapes fused. There were a few seconds of violent splashing but no sign of blood. The shark disappeared.

The two seals continued to move towards shore, the adult again circling the subadult. The adult frequently lifted its head high and looked around. Twice it abandoned the subadult to haul out briefly on the beach. Both seals finally reached the shoreline and remained there 2 min. The subadult raised its head but did not haul out. The adult hauled out briefly on the beach but followed the subadult when it moved offshore again.

Second attack—At 1947 h the seals were together about 5 m offshore when a large fin appeared north of them. The fin moved slowly and steadily south directly towards the seals. Again the adult seal rapidly swam between the subadult and approaching shark and the fin disappeared. The adult seal immediately hauled out, then briefly returned to the subadult in the water but stayed on the shoreside and did not circle. The adult hauled out again and remained on the beach.

Fatal attack—At 1957 h, approximately 4 min after the adult seal left it, the subadult rested alone on water 3–6 m deep over sandy bottom, 23–30 m south of where the first attack was observed. A large submerged shark approached from the south. Suddenly there was violent splashing as the subadult was pulled under in a single motion and replaced on the surface by a cloud of blood. The fins of at least 10 small sharks immediately appeared, circling within a 15 m radius. These sharks were an estimated total length of 1.5–1.8 m and were presumed to be gray reef sharks, *Carcharhinus amblyrhynchos,* based on coloration, size and known abundance in the Laysan area. Large fins were not seen. Within 2.5 min after the fatal attack, the blood dissipated and the small fins began to disperse. A few frigate birds, *Fregata minor,* dived into the water 15 min after the attack. Twenty-eight minutes after the attack, the forms of two large sharks and 20 or more small dorsal fins were seen in the immediate vicinity. An adult seal swimming north passed within a meter of the small sharks, and both species appeared to ignore each other. A minute later the dorsal surfaces and dorsal and caudal fins of two large tiger sharks (estimated total lengths 3.5 and 5.0 m) simultaneously surfaced. Observations were terminated by rain and darkness.

There are three aspects of these observations that are of particular interest. First, they confirm that sharks do not merely scavenge or injure monk seals but kill them. Second, the adult seal's "attack" on the large approaching shark exemplifies the aggressiveness of adult male monk seals during the breeding season. Aggressive behavior of adult males towards large tiger sharks has also been seen on nearby Lisianski Island (T. Loughlin and G. Kooyman, pers. comm., Johanos and Kam 1986). Third, the combined presence of large predators and injured seals (frequently females with adult male inflicted injuries) indicates that females at some locations may be more prone to shark predation. Fatal shark attacks could contribute to the monk seal population decline at these locations, both through direct fatalities and due to reduced natality when females are the victims. This can have dire consequences for this species whose counts since 1958 indicate a low and declining total population (Johnson *et al.* 1982).

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EL ZOOPLANCTON DEL PACIFICO ECUATORIANO

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y

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RESUMEN

La distribución de las especies de Quetognatos, Sifonóforos, Medusas, Ctenóforos y larvas de peces se basa en el análisis del material de plancton recolectado durante la Expedición SWAN SONG en la región de las Islas Galápagos, en los meses de octubre y noviembre de 1961. Los Quetognatos están representados por 19 especies que corresponden a las categorías ecológicas trópico-ecuatoriales del Pacífico e Indico y *Sagitta pacifica;* especies típicas de aguas templadas y cálidas del Atlántico, Pacífico e Indico y *Sagitta bierii* que habita principalmente las zonas de las Corrientes de Perú y California, y además especies meso-batipelágicas (*Eukrohnia hamata*, *Heterokrohnia mirabilis*, *Sagitta decipiens*, *S. maxima*, *S. zetesios*). Se obtuvieron 26 especies de Sifonóforos, típicos del cinturón trópico-ecuatorial, cosmopolitas, y de régimen nerítico (*Muggiaea kochi*). Las medusas incluían también especies trópico-ecuatoriales y cosmopolitas, y las Escifomedusas *Pelagia noctiluca* y *P. flaveola*. *Beroë forskale* ha sido el único Ctenóforo observado en estas colecciones. Las especies de larvas de peces corresponden a las familias, Carangidae, Carapidae, Moridae, Bathylagidae, Nomeidae, Myctophidae, Gonostomatidae, Antennaridae, Sternoptychidae, Idiacanthidae, Ogcocephalidae, Clupeidae, Cynoglossidae, Melanostomiatidae, Paralepididae, Melanocetidae, y los Leptocephalus. Se discuten en particular las especies indicadoras de las corrientes que fluyen por esa región, y la identificación de aguas de surgencia mar afuera al oeste de las Islas, al NW de Isla Isabela y en la zona entre las islas y el continente.

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ABSTRACT

Distribution and abundance of species of Chaetognatha, Siphonophorae, Medusae, Ctenophora and Fish larvae are based on the study of plankton collections obtained during the SWAN SONG Expedition in the Galapagos Islands region, October-November, 1961. Chaetognatha are represented by 19 species belonging to the tropico-equatorial Indo-Pacific; typical of the Atlantic, Pacific and Indian Oceans temperate and warm waters, and *Sagitta bierii* (species inhabiting the American Pacific, mainly the Peru and California Current regions), and the meso-bathypelagic species *Eukrohnia hamata, Heterokrohnia mirabilis, Sagitta decipiens, S. maxima, S. zetesios*. Siphonophorae are distributed into 26 species, belonging to tropico-equatorial and cosmopolitan regions, and the Scyphomedusae *Pelagia noctiluca* and *P. flaveola*. *Beroë forskale* was the only Ctenophora found. Fish larvae species are included in the families Carangidae, Carapidae, Moridae, Bathylagidae, Nomeidae, Myctophidae, Gonostomatidae, Stermoptichidae, Idiacanthidae, Ogcocephalidae, Clupeidae, Cynoglossidae, Melanostomiatidae, Paralepididae, Melanocetidae, and species of *Leptocephalus*. Indicator species of currents in the region are discussed, and their use to detect changes in the ocean dynamics. Upwelled waters were identified off western area from the Islands, NW of Isabella Islands, and in the region between the Archipelago and the continent.

INTRODUCCION

El material de plancton analizado se recolectó en la región de las Islas Galápagos durante la Expedición SWAN SONG. Las colecciones fueron obtenidas en los meses de octubre y noviembre de 1961. Se han estudiado los Quetognatos, Sifonóforos, Medusas, Ctenóforos, alevines y larvas de peces.

Los estudios previos efectuados en esta región y zonas adyacentes en relación con los grupos mencionados, se discuten en, Agassiz y Mayer (1902), Ahlstrom (1971, 1972), Ahlstrom y Counts (1958), Ahlstrom y Moser (1969), Ahlstrom, Butler, Sumida (1976), Alvariño (1962, 1964, 1965, 1970, 1971, 1972, 1974, 1976 a,b), Beebe y Vander Pyl (1944), Bieri (1957), Bigelow (1909, 1911, 1912, 1928, 1931, 1940), Bonilla (1938 a, b), Garman (1899), Grey (1960), Haedrich (1966, Heller y Snodgrass (1903), Hildebrand (1946), Horn y Haedrich (1973), Hubbs (1958), Jiménez (1978), Kramp (1956, 1968), Maas (1897), Mayer (1910), Morrow (1957 a,b), Parin (1968), Pineda (1968, 1969), Sandoval de Castillo (1984), Santander y de Castillo (1969), Segura (1984), Sund (1961 a,b, 1964), Sund y Renner (1959), Vanhöffen (1913), Wisner (1971, 1977).

La región de las Islas Galápagos se encuentra bajo la influencia directa de La Corriente Ecuatorial Meridional y corriente Submarina, recibiendo también avances de la Corriente de Perú y la Contracorriente Ecuatorial. En las inmediaciones de las Islas Galápagos se observan a veces fuertes surgencias, y las aguas de advección procedentes de este fenómeno se extienden por la región. El estudio del plancton definir las especies que señalan las distintas influencias oceánicas en la región.

Las aguas oceánicas de esta zona mantienen prácticamente la misma temperatura desde la superficie hasta los 30 m de profundidad. En la serie de Estaciones a lo largo del meridiano 96°W al oeste de las Islas Galápagos, la temperatura en ese estrato de 30 m de profundidad era de 26°5C en las localidades más nórdicas ocupadas durante la exploración; mientras que en la zona más meridional la temperatura en los estratos alcanzaba entre los 21°C hasta los 15°C. En la serie de localidades ocupadas a lo largo del meridiano 87°W al este de las Islas, la temperatura de la capa de 30 m a la superficie era de 26°3C en las estaciones más nórdicas, disminuyendo progresivamente hasta 18°C frente a las Islas, por efecto de surgencia de aguas profundas, para aumentar hasta 21°C hacia el sur. Dichas aguas de superficie que abarcan un estrato de 30 m de altura, presentan por debajo un lecho de discontinuidad muy acusado, donde la temperatura decrece rápidamente. Así, entre los 30 m y 50 m de profundidad existe un cambio tan brusco de temperatura, que la termoclina presenta con frecuencia un gradiente de 9°C o más, con respecto a las capas superiores, (Figs. 2 y 4).

La salinidad es constante hasta los 30 m de profundidad en los perfiles a lo largo de los meridianos 96°W y 87°W, respectivamente al oeste y este de las Islas. Desde los 30 m de profundidad la salinidad aumenta hasta los 250 m, 100 m ó 75 m de profundidad, después de ese nivel disminuye otra vez, pero manteniéndose siempre a más de 34 o/oo. Un fuerte avance de aguas de salinidad 35 o/oo se observa en la parte sur del perfil oriental, señalando una corriente submarina, que también se reconoce en el perfil occidental. (Figs. 3 y 5).

El frente oceánico que separa las aguas tropicales y las de la Corriente de Perú se acusa más durante el período de mayo a noviembre (Wyrtki 1966). Frentes oceánicos, remolinos, configuración del fondo y del litoral alteran la distribución de los organismos marinos, de tal forma que con frecuencia la acumulación de poblaciones en una zona no se debe solamente a procesos biológicos, sino también a la acción de la circulación oceánica. Los frentes producen zonas de surgencia y de sumersión de aguas, mientras que los remolinos constituyen una circulación cerrada en áreas donde la circulación horizontal se produce o se mantiene, así como también en torno a las islas y bajos. Las islas constituyen un obstáculo en la circulación con fractura del equilibrio, produciéndose un remolino que persiste, aunque variando en magnitud con los vientos. Así, en las Islas Galápagos, también existen remolinos al este, en relación con la corriente submarina ecuatorial.

La combinación de las corrientes, frentes, surgencias, sumersiones, remolinos, y la actividad de los organismos, producen una cadena de efectos ecológicos. Muchos de los organismos son observados en las colecciones debido a la acción de algunos de los fenómenos señalados. Los animales nadan, flotan, se sumergen y se reproducen, proliferando o desapareciendo a causa de los factores ambientales, alimentación, depredación, etc. Los frentes oceánicos con los procesos dinámicos resultantes y los remolinos afectan a la distribución de los organismos, aglomerando poblaciones que normalmente no se encontrarían en contacto, constituyéndose así nuevas comunidades, conservándose y disociándose componentes de poblaciones de especies y su respectiva abundancia, manteniéndose las poblaciones en ciertas zonas que resultan adecuadas para la reproducción, limitando y activando además la dispersión, y modificando también el régimen migratorio de algunas especies. Estos efectos se observarán en este estudio y se discuten al analizar la distribución de las especies.

MATERIAL Y METODO

Las colecciones de plancton de la Expedición SWAN SONG han sido obtenidas con redes Clarke-Bumpus y redes cónicas de 1 m de diámetro en la boca. Las pescas con redes Clarke-Bumpus se efectuaron en arrastres horizontales a diversos niveles de profundidad, que oscilaban entre 3 m y 160 m. Las pescas con red de 1 m se utilizaron en arrastres oblicuos, desde diversas profundidades hasta la superficie oceánica.

Con la red Clarke-Bumpus se realizó un total de 16 arrastres, distribuidos en siete localidades, y con la red de 1 m se ocuparon 16 localidades, con un total de 18 arrastres, oscilando entre los 190 m y 448 m de profundidad hasta 0 m (Fig. 1, Tabla 1).

En la Tabla 1 se incluyen datos correspondientes a cada lance para recolectar plancton. Los valores numéricos de abundancia para cada especie se han normalizado, excepto en dos arrastres horizontales a 55 m de profundidad en las Estaciones 24 y 25, cuando no se han conseguido datos sobre el agua filtrada. Los resultados cuantitativos para las especies capturadas se han normalizado

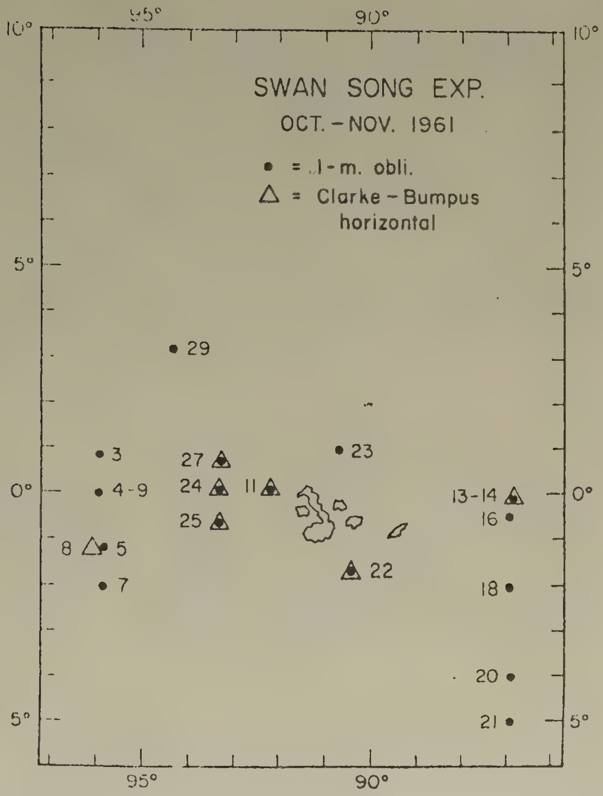


Fig. 1. Mapa con la distribución de las Estaciones correspondientes a la Expedición SWAN SONG.

en cada caso para 1000 m^3 de agua filtrada por las redes, y así se presentan en tablas y mapas de distribución.

En el caso de los Sifonóforos, la abundancia se calcula para los Diphyidae, Clausophyidae y Abylinae, considerando el mayor número obtenido, ya sea de nectoforos superior o inferior (fase poligástrica) y de brácteas o gonoforos (fase de eudoxia). En otras familias de Calcycophorae, se emplearon otros métodos para determinar la densidad de población. Por ejemplo, en los Hippopodidae, un organismo puede constar de unos 10 a 13 nectoforos. En el caso de los Cystonectae y Physonectae, solamente el número de pneumatoforos indicará la cantidad de animales, y las brácteas y nectoforos únicamente señalan la presencia de la especie.

La información hidrográfica obtenida durante la Expedición SWAN SONG aparece en Data Report, SWAN SONG Expedition, Physical, Chemical, Current measurements and Biological data, Scripps Institution of Oceanography, Ref. 66-1 Universidad de California, 15 de septiembre de 1965, páginas 1-125.

La distribución de algunas especies se presenta en mapas indicando los valores cuantitativos mediante contornos que incluyen exclusivamente las capturas oblicuas. Las observaciones positivas de los arrastres horizontales se presentan por trazos cortos sobre el triángulo que marca la ESTACION, de modo que las unidades se indican por un trazo, decenas por dos, centenas por tres, unidades de millar por cuatro y concentraciones de más de decenas de millar por el signo > . La densidad de población para los arrastres oblícuos se identifica mediante la clave que se inserta en el mapa.

Los dos tipos de arrastre empleados para recolectar el plancton son muy distintos, y así los datos obtenidos no pueden compararse directamente. Sin embargo, mediante las colecciones horizontales se ha podido obtener información sobre la distribución batimétrica que presentan algunas especies en esta región, y los efectos de la termoclina y frentes oceánicos, con los procesos dinámicos de surgencia, sumersión y remolinos.

LOS QUETOGNATOS DE LA REGION DE LAS ISLAS GALAPAGOS.

El material estudiado incluye diez y nueve especies que corresponden a las categorías trópico-ecuatoriales del Pacífico e Indico (*Krohnitta pacifica, Sagitta bedoti, S. ferox, S. neglecta, S. pulchra, S. robusta*) y *S. pacifica* que avanza desde esa región hacia las zonas templadas adyacentes. Las especies cosmopolitas del Atlántico, Pacífico e Indico (*K. subtilis, Pterosagitta draco, S. bipunctata, S. enflata, S. hexaptera, S. minima*). Especies meso-batipelágicas *Eukrohnia hamata, Heterokrohnia mirabilis, S. decipiens, S. maxima, S. zetesios*) y la especie típica del Pacífico Americano, *S. bierii*, característica principalmente de las zonas que abarcan las corrientes de California y Perú.

Todas las especies de Quetognatos obtenidas en las colecciones han sido observadas previamente en la región. Hay que notar la ausencia de *S. regularis* (típica de la región trópico ecuatorial Indo-Pacífica), y las especies neríticas de la región trópico-ecuatorial del Pacífico americano, *S. popovicii* y *S. peruviana*. Los individuos de estas tres especies son de talla pequeña y pudieran facilmente filtrarse a través de las mallas de las redes empleadas. (Tablas 2 y 3).

En las pescas horizontales efectuadas a profundidades que oscilaban entre 3 m y 160 m no se han encontrado, *E. hamata, S. ferox, S. maxima, S. neglecta, S. robusta, S. zetesios*. En muchos casos la ausencia de una de esas especies se puede relacionar con la profundidad del arrastre, pero la carencia de representantes de las especies epipelágicas *S. ferox*, *S. neglecta*, *S. robusta* ha de estar relacionada con las características particulares de los arrastres horizontales y la velocidad de los mismos (Tabla 2). En los arrastres horizontales se ha de abarcar precisamente el estrato habitado por la especie durante el período del arrastre para que aparezcan sus representantes en la muestra, y únicamente cuando los arrastres horizontales se efectuan a varios estratos de profundidad en la misma localidad, se puede llegar a ocupar la banda habitada por cada especie. Este problema se evita mediante los arrastres oblicuos.

Las colecciones de arrastre horizontal incluyen solamente 13 especies. La más abundante *S. enflata*, seguida por *Pterosagitta draco*, *S. bedoti*, *S. pacifica*. La especie más frecuente también resultó ser *S. enflata*, seguida por *S. hexaptera* y *S. pacifica*. La mayor abundancia de *K. pacifica* se observó a los 10 m de profundidad, *S. enflata* entre 10 y 20 m junto con otras especies (Tabla 2). A los 100 y 160 m de profundidad se obtuvieron representantes de las especies meso-batipelágicas. *S. decipiens* se observó en arrastres a 3 m, 10 m, 35 m, 42 m, 75 m y 100 m de profundidad en zonas de surgencia y áreas que alcanzan las aguas de advección procedentes de la surgencia. *H. mirabilis* se encontró en la Estación 25, en arrastre horizontal a 160 m de profundidad, en una zona al oeste de las islas, marcada por una fuerte surgencia (Figs. 2 y 4).

En los arrastres oblicuos, las profundidades oscilaban entre 190 m y 448 m hasta la superficie oceánica. En estas colecciones se obtuvieron representantes de todas las especies de Quetognatos mencionados, a excepción de *H. mirabilis*. En estas muestras la especie más abundante ha sido también *S. enflata*, seguida en orden decreciente de abundancia, por *S. bedoti*, *S. pacifica*, *S. hexaptera*, *S. bierii* (Tabla 3). Las especies más frecuentes, resultaron *S. enflata* y *S. hexaptera*, seguidas por *S. bedoti*, *P. draco* Y *S. pacifica*.

Krohnitta pacifica se presentaba abundante al SE, NW y oeste de las islas, (Fig. 6), indicando la presencia de aguas tropicales, y se nota que la fuerte termoclina no afecta la distribución batimétrica de esta especie en esta zona.

Pterosagitta draco estaba bien distribuida por la región explorada, con máximos al nordeste de las Islas Galápagos, (Fig. 7). Una distribución similar la presentaba *K. subtilis*, aunque con densidad de población más baja.

Sagitta bedoti se encontró con una población abundante que abarca toda la región, avanzando hacia las islas desde el oeste y

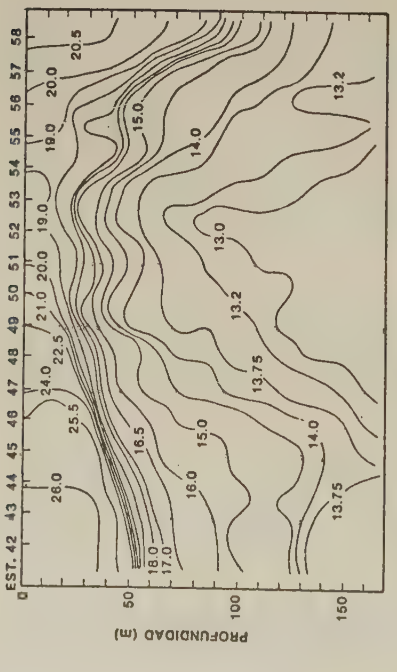


Fig. 2. Perfil con la distribución batimétrica de isotermas en las Estaciones a lo largo.

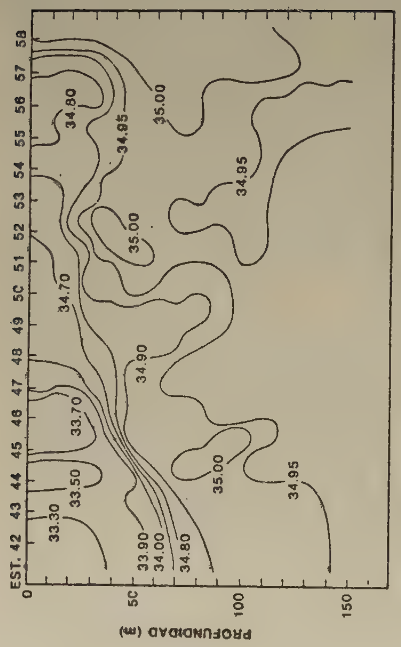


Fig. 3. Perfil con la distribución batimétrica de isohalinas en las Estaciones a lo largo.

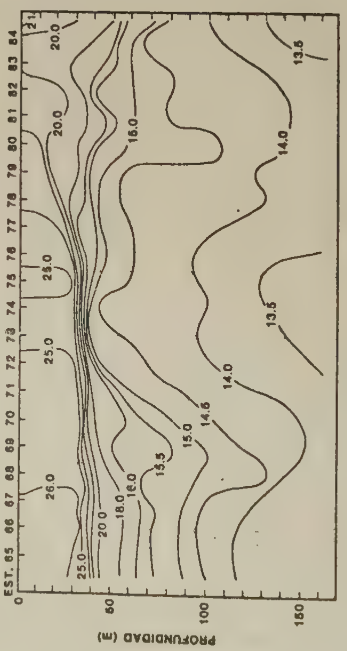


Fig. 4. Perfil con la distribución batimétrica de isotermas en las Estaciones a lo largo del Meridiano 87°W.

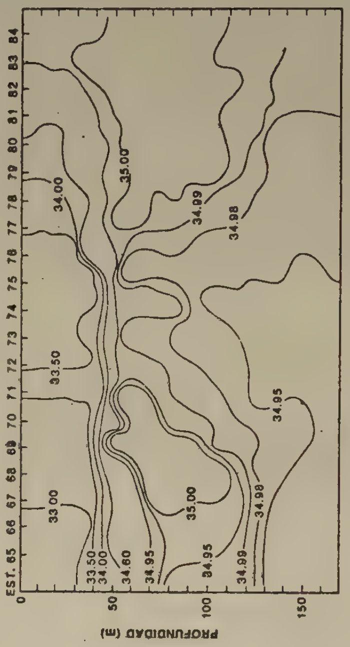


Fig. 5. Perfil con la distribución batimétrica de ishohalinas en las Estaciones a lo largo del Meridiano 87°W.

el este, indicando el alcance y dominancia de las aguas tropicales en la región (Fig. 8).

Sagitta bierii estaba distribuida a lo largo de una franja que avanzaba desde el oeste sin llegar a ocupar en general, las zonas habitadas por S. *enflata* y S. *hexaptera*. *Sagitta bierii* corresponde a la corriente de Perú, aguas distintas a las que caracterizan a S. *enflata* y S. *hexaptera*, que al parecer no se mezclan en la mayor parte de la zona investigada. (Fig. 9).

La distribución de S. *decipiens* marca una zona amplia que se extiende al oeste y este de las Islas. Las poblaciones de S. *decipiens* proceden originalmente de zonas de fuertes surgencias, avanzando con las aguas hacia otras localidades mediante mecanismos de advección. La distribución de esta especie y S. *bierii* resulta en lineas generales coincidente. (Fig. 10). Los perfiles hidrográficos señalan perfectamente la afloración de aguas submarinas.

Sagitta enflata presentaba un núcleo de población de elevada densidad entre el continente y las Islas Galápagos, avanzando progresivamente mar afuera y decreciendo así también en abundancia. (Fig. 11).

Las poblaciones de S. *ferox* se extendían desde centros básicos al este y oeste de las islas, pero sin adentrarse en la propia zona insular. Igualmente se puede señalar para S. *hexaptera*, aún cuando esta especie se presentaba más abundante y sus poblaciones cubrían toda la zona explorada. (Figs. 12 y 13). S. *ferox* es una especie típica tropical, mientras que S. *hexaptera* es cosmopolita, no acusando así las limitaciones del habitat para la distribución de sus poblaciones.

Así como S. *decipiens* marcaba una zona de surgencias en la región, también este fenómeno es acusado por la presencia de S. *zetesios* en la Estación 3, las poblaciones de S. *maxima* extendiéndose al este y oeste del archipiélago, cubrían una zona de divergencia, marcada por el afloramiento de aguas profundas. Sin embargo, S. *maxima* no se ha obtenido en las pescas horizontales, y su presencia en los arrastres oblicuos estaría determinada por la profundidad de esos arrastres, aún cuando en la Estación 18, desde 190 m de profundidad también se ha encontrado representada esa especie. (Fig. 14).

Las poblaciones de S. *minima* y E. *hamata* mostraban una distribución similar, considerando solamente las colecciones oblicuas, encontrándose en el sureste y noroeste de la región. (Fig. 15). Sin embargo, la primera de estas especies se obtuvo además

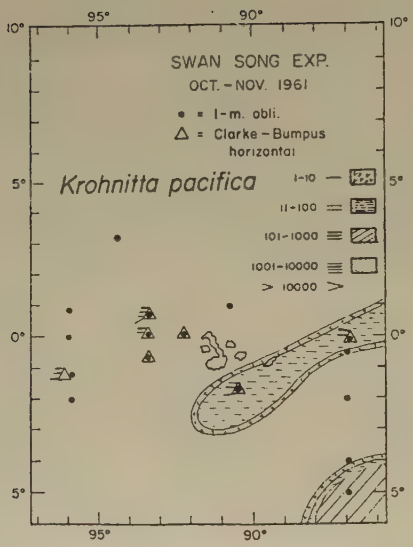
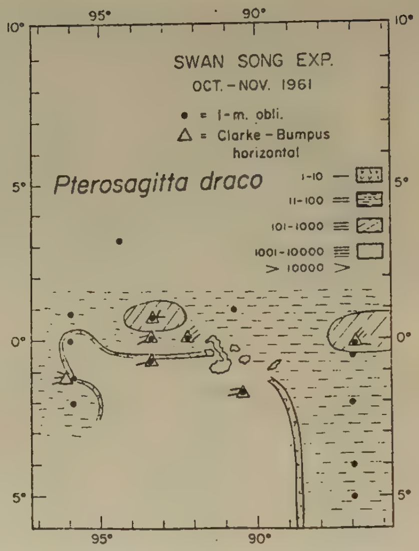

95°
90°
10°
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Krohnitta pacifica
1-10
11-100
101-1000
1001-10000
> 10000
5°
0°
5°
95°
90°

Fig. 6. Distribución de *Krohnitta pacifica* en la región de las Islas Galápagos.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OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Pterosagitta draco
1-10
11-100
101-1000
1001-10000
> 10000
5°
0°
5°
95°
90°

Fig. 7. Distribución de *Pterosagitta draco* en la región de las Islas Galápagos.

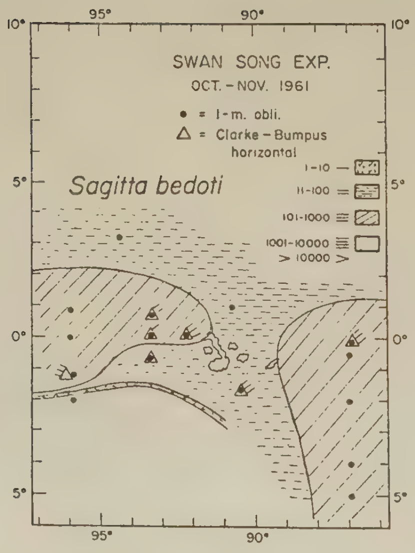
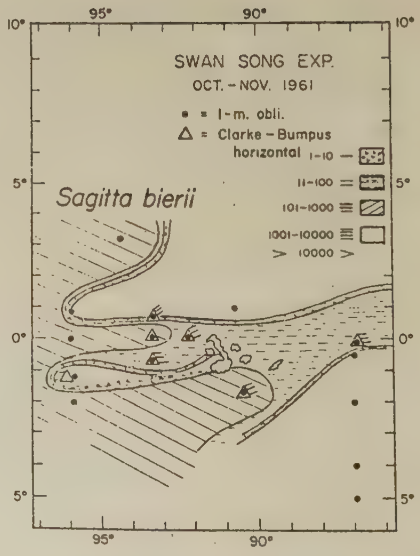

95°
90°
10°
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Sagitta bedoti
1-10
11-100
101-1000
1001-10000
> 10000
5°
0°
5°
95°
90°

Fig. 8. Distribución de *Sagitta bedoti* en la región de las Islas Galápagos.


95°
90°
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SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Sagitta bierii
1-10
11-100
101-1000
1001-10000
> 10000
5°
0°
5°
95°
90°

Fig. 9. Distribución de *Sagitta bierii* en la región de las Islas Galápagos.

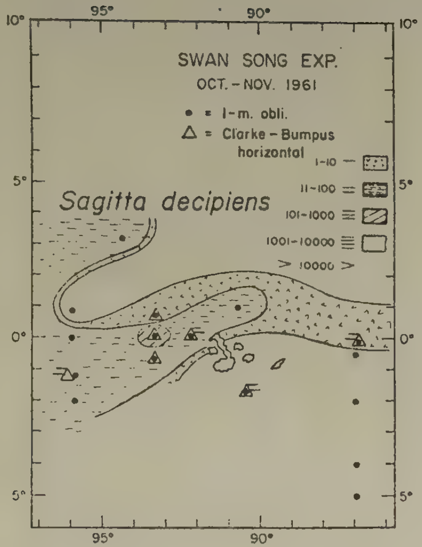

SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
1-10
11-100
101-1000
1001-10000
> 10000 >
Sagitta decipiens
95°
90°
10°
5°
0°
5°

Fig. 10. Distribución de *Sagitta decipiens* en la región de las Islas Galápagos.

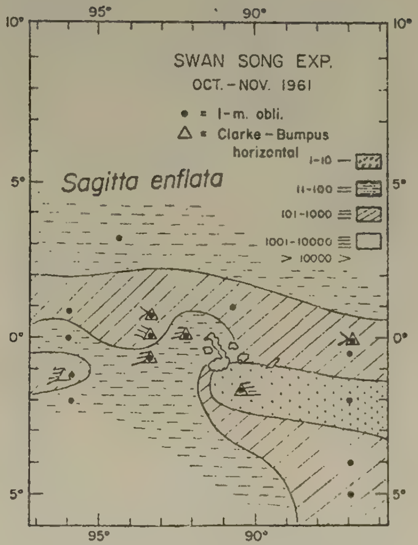

SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
1-10
11-100
101-1000
1001-10000
> 10000 >
Sagitta enflata
95°
90°
10°
5°
0°
5°

Fig. 11. Distribución de *Sagitta enflata* en la región de las Islas Galápagos

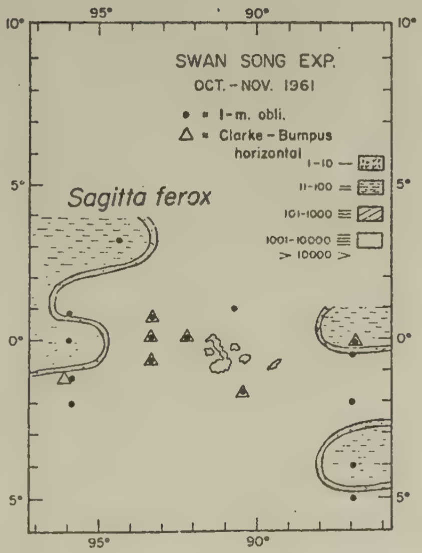

SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
1-10
11-100
101-1000
1001-10000
> 10000 >
Sagitta ferox
95°
90°
10°
5°
0°
5°

Fig. 12. Distribución de *Sagitta ferox* en la región de las Islas Galápagos.

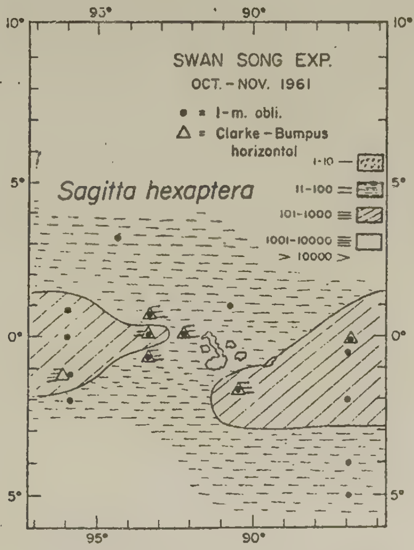

SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
1-10
11-100
101-1000
1001-10000
> 10000 >
Sagitta hexaptera
95°
90°
10°
5°
0°
5°

Fig. 13. Distribución de *Sagitta hexaptera* en la región de las Islas Galápagos.

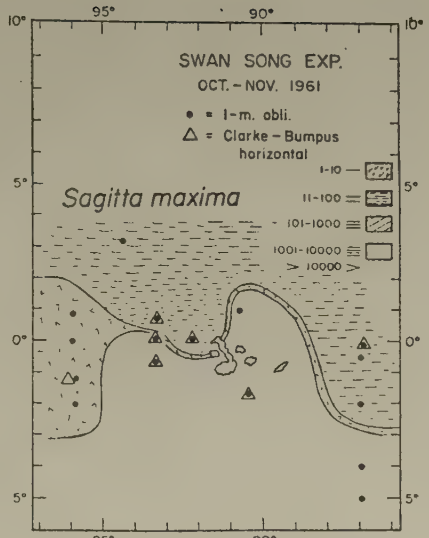
en las pescas horizontales, mientras que *E. hamata* (meso-batipelágica en esta región) solo se presentaba en las pescas oblicuas y en número reducido de ejemplares, en arrastres desde 227 m y 448 m de profundidad hasta la superficie oceánica, donde los estratos que habita la especie emergen hasta profundidades más cerca de la superficie oceánica.

Las poblaciones de *S. neglecta* y *S. pulchra* avanzan desde la parte oriental (Figs. 16 y 17). y *S. pacifica* marcaba una progresión al nordeste y este de la región, extendiéndose con abundancia relativamente elevada. (Fig. 18).

Sagitta robusta se observó en escaso número y solamente en la Estación 23, en una pesca oblicua desde 369 m de profundidad. *S. bipunctata* (indicadora de aguas del Pacífico Central) se obtuvo únicamente en un arrastre horizontal a 10 m. de profundidad en la Estación 27. *Heterokrohnia mirabilis* es una especie de la cual existen datos esporádicos sobre su distribución y raramente se captura, de modo que el hallazgo en la Estación 25 en un arrastre horizontal a 160 m de profundidad, es interesante para añadir a los pocos datos que existen de esta especie.

Las aguas tropicales están señaladas por las especies típicas en la región. Indicios de mezcla con aguas de la corriente de Perú se representan por *S. bierii*, aguas del Pacífico Central por *P. draco* y *S. bipunctata*, y las demás especies son de presencia casi constante en todo el ámbito de las aguas templadas y cálidas de los océanos. Areas de surgencia y sus aguas están indicadas por las especies meso-batipelágicas presentándose a niveles batimétricos más cercanos a la superficie oceánica.

La fuerte termoclina no afecta, al parecer, la distribución batimétrica de algunas especies. *S. enflata* y *S. hexaptera* se observaron en todos los arrastres por encima, debajo y en la banda de la termoclina. *K. pacifica* y *K. subtilis* se obtuvieron en la Estación 22 a 3 m, 15 m y a 70 m, así como en la Estación 27. Sin embargo, *P. draco* solamente se presentó sin limitaciones aparentes en relación con la termoclina, en la Estación 27, y en las demás localidades se observó en estratos por encima de la discontinuidad térmica. *S. bedoti* y *S. bierii* únicamente se observaron independientemente de la termoclina en dos estaciones, y las demás especies presentan al parecer alguna limitación en su distribución batimétrica en la zona y circunstancias presentes durante el período de esta exploración.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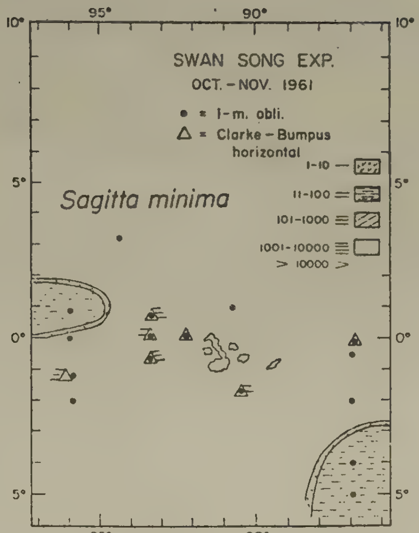
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Sagitta maxima
1-10
11-100
101-1000
1001-10000
> 10000 >

Fig. 14. Distribución de *Sagitta maxima* en la región de las Islas Galápagos.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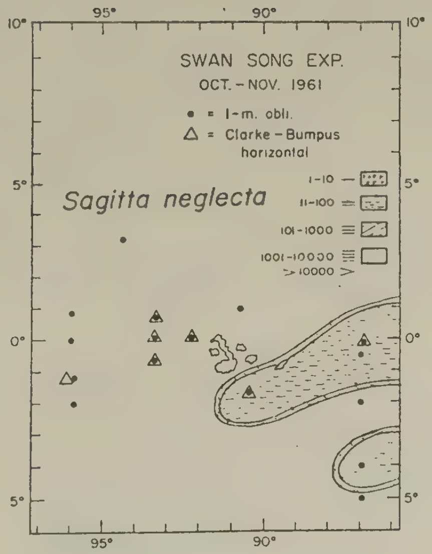
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Sagitta minima
1-10
11-100
101-1000
1001-10000
> 10000 >

Fig. 15. Distribución de *Sagitta minima* en la región de las Islas Galápagos.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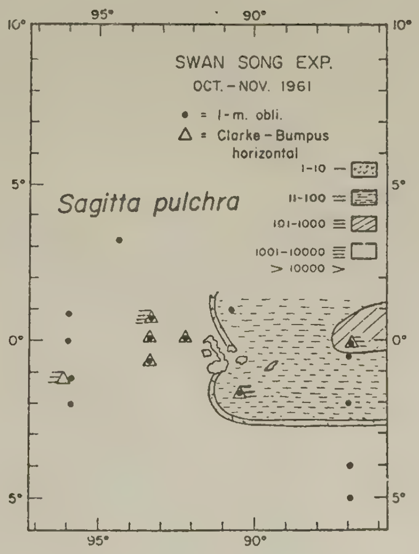
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Sagitta neglecta
1-10
11-100
101-1000
1001-10000
> 10000 >

Fig. 16. Distribución de *Sagitta neglecta* en la región de las Islas Galápagos.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SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Sagitta pulchra
1-10
11-100
101-1000
1001-10000
> 10000 >

Fig. 17. Distribución de *Sagitta pulchra* en la región de las Islas Galápagos.

LOS SIFONOFOROS DE LA REGION DE LAS ISLAS GALAPAGOS.

Se ha determinado un total de 26 especies, de las cuales solamente 13 resultaron comunes para ambos métodos de captura. En las pescas horizontales se obtuvieron 16 especies y 24 en los arrastres oblicuos (Tablas 4 y 5).

Los sifonóforos característicos del cinturón trópico-ecuatorial observados en estas colecciones, han sido, *Chelophyes contorta*, *Diphyopsis mitra*, *Lensia campanella*, *L. hotspur*, *Sulculeolaria bigelowi*, *S. monoica*, *S. turgida*, *Ceratocymba sagittata*, *Abylopsis eschscholtzi*, *A. tetragona*, *Vogtia kuruae*, *V. spinosa*, *Amphicaryon ernesti*, *Bargmannia elongata*, *Nectodroma reticulata*, de las cuales, las cinco últimas se observan también en aguas templadas. Además se han observado especies cosmopolitas características de las regiones templadas y cálidas oceánicas (*Chelophyes appendiculata*, *Diphyes bojani*, *D. dispar*, *S. quadrivalvis*, *Hippopodius hippopus*, *Agalma okeni*, *Stephanomia bijuga*, *Physophora hydrostatica*, *Rosacea cymbiformis*), y la especie nerítica de las regiones trópico-ecuatoriales del Atlántico y Pacífico, *Muggiaea kochi*, así como *Lensia challengeri* que es abundante en aguas templadas de los Océanos Pacífico e Indico.

Chelophyes contorta resultó la especie más abundante en las pescas horizontales, con 7571 ejemplares en una Estación donde el arrastre abarcaba el estrato de los 10 m de profundidad, seguida en número decreciente por *M. kochi*, *Ch. appendiculata* y la fase poligástrica de *D. mitra*. La frecuencia de estas poblaciones en la zona correspondía en orden decreciente a, *M. kochi*, *Ch. appendiculata* y *D. mitra*.

En los arrastres oblicuos la especie más abundante ha sido *L. challengeri*, seguida por *D. mitra* y *Ch. appendiculata*. Las especies más frecuentes en orden decreciente fueron, *L. challengeri*, *D. mitra* con *Ch. appendiculata* y *A. tetragona* a igualdad de magnitud.

Once de las especies incluidas en el número total de sifonóforos no aparecieron en las pescas horizontales, debido posiblemente a las causas señaladas anteriormente respecto a la inconveniencia de este tipo de arrastres. Hay que indicar además, que no se han encontrado sifonóforos en las colectas horizontales de las Estaciones 14, 22, 24, respectivamente a 20 m, 3 m y 55 m de profundidad. Sin embargo, tres especies, *D. bojani*, *L. campanella*, *R. cymbiformis* no se observaron en las colecciones procedentes de arrastres oblicuos. Hay que tener en cuenta que, los sifonóforos no presentan una distribución tan continua como otros elementos del plancton, y se caracterizan por una distribución errátil y discontinua.

Muggiaea kochi habita la zona nerítica del continente adyacente a las Islas Galápagos y sus poblaciones avanzan hasta el archipiélago y se adentran desde ahí hasta localidades mar afuera. (Fig. 19).

Es notable la presencia en esta región de la pareja de especies de *Chelophyes*, con dominio de la especie cosmopolita *Ch. appendiculata* sobre la tropical *Ch. contorta*. Sin embargo, las poblaciones de *Ch. appendiculata* abarcan la extensión hacia el oeste, sureste y este de las islas, avanzando únicamente hacia el archipiélago en tres ocasiones, presentándose en estratos a 35 m y 15 m de profundidad, mientras que *Ch. contorta* extendía sus poblaciones ampliamente por la región norte y este de las islas conjuntamente con la dominancia de las aguas tropicales. (Figs. 20 y 21).

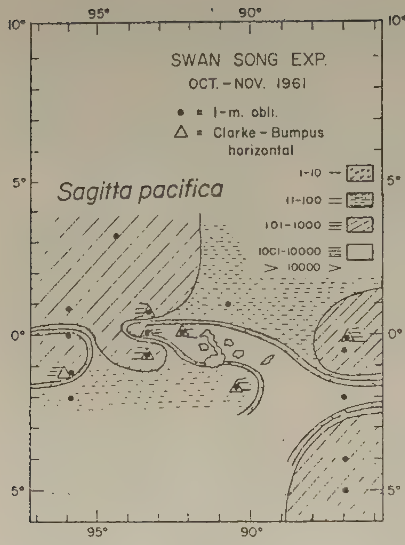
Entre los Diphyinae se observaron, *D. bojani*, *D. dispar*, *D. mitra*; de estas especies, la última presentaba poblaciones densas (Fig. 22); ya que las otras se encontraban diseminadas y esparcidas por la región. Esto indica asimismo, la dominancia del régimen tropical en la zona. *D. bojani* se observó únicamente en las colecciones horizontales a 11 m y 55 m de profundidad, y *D. dispar* se encontró en una muestra a 11 m de profundidad y en arrastres oblícuos efectuados desde 386, y 245 m respectivamente en las Estaciones 4 y 16.

El género *Lensia* estaba representado por *L. campanella*, *L. challengeri* y *L. hotspur*. La primera es tropical y se presentaba en un arrastre horizontal a 42 m de profundidad. *L. challengeri* se extendía por toda la región, encontrándose tanto en los arrastres horizontales como oblicuos (Fig. 23), y *L. hotspur* se observó solamente en una pesca oblícua desde 190 m de profundidad.

El género *Sulculeolaria* estaba representado por cuatro especies diseminadas por unas pocas Estaciones, observándose particularmente en las colectas oblicuas, aunque *S. begelowi* se obtuvo en un arrastre horizontal a 10 m de profundidad. Las especies más abundantes de este género en la región son las de régimen tropical, *S. bigelowi*, *S. monoica*, *S. turgida*.

Abylopsis eschscholtzi y *A. tetragona* aparecen esparcidas con dominancia de la última tanto en arrastres oblicuos como horizontales, mientras que la primera se observó solamente en la Estación 9 correspondiente a un arrastre oblicuo (Fig. 24).

Ceratocymba sagittata es una especie poco frecuente y abundante en todos los océanos, observándose durante este estudio en una pesca oblicua desde 277 m de profundidad.



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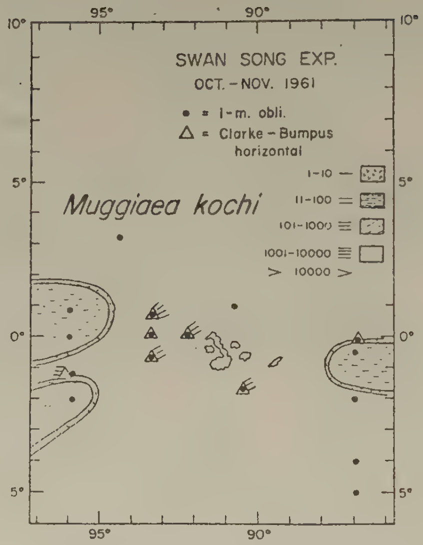
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Sagitta pacifica
1-10 —
11-100 =
101-1000 ≡
1001-10000 ≣
> 10000 >

Fig. 18. Distribución de *Sagitta pacifica* en la región de las Islas Galápagos.



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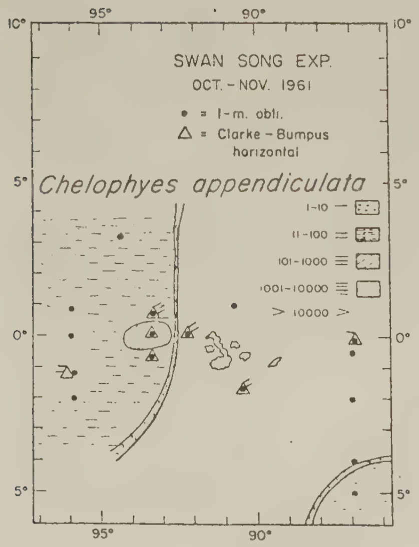
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Muggiaea kochi
1-10 —
11-100 =
101-1000 ≡
1001-10000 ≣
> 10000 >

Fig. 19. Distribución de *Muggiaea kochi* en la región de las Islas Galápagos.



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SWAN SONG EXP.
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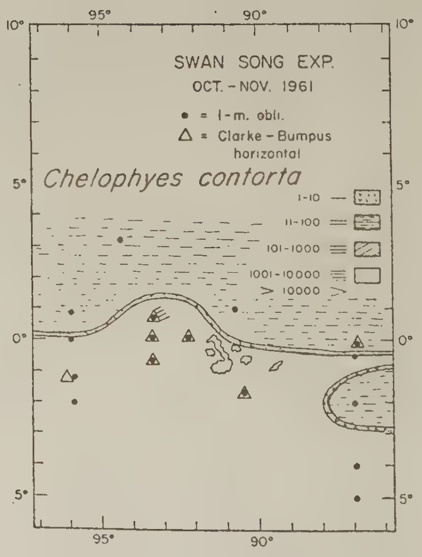
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Chelophyes appendiculata
1-10 —
11-100 =
101-1000 ≡
1001-10000 ≣
> 10000 >

Fig. 20. Distribución de *Chelophyes appendiculata* en la región de las Islas Galápagos.



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SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Chelophyes contorta
1-10 —
11-100 =
101-1000 ≡
1001-10000 ≣
> 10000 >

Fig. 21. Distribución de *Chelophyes contorta* en la región de las Islas Galápagos.

De la familia *Hippopodidae* se obtuvieron tres especies, *H. hippopus*, *Vogtia kuruae* y *V. spinosa*. La primera es cosmopolita y las otras dos típicas de aguas más cálidas. *H. hippopus* y *V. spinosa* presentaban distribución similar en toda la región, (Figs. 25 y 26); mientras que *V. kuruae* aparecía con tres colonias en la Estación 16 en un arrastre oblicuo.

La Subfamilia *Prayinae* se destaca por la presencia de *Rosacea cymbiformis* en la Estación 11 a 100 m de profundidad, y *N. reticulata* en un arrastre oblicuo desde 301 m de profundidad.

Amphicaryon ernesti es la única especie de la Subfamilia *Amphicaryonidae* representada por cinco colonias en un arrastre desde 329 m de profundidad.

La familia *Physophoridae* estaba representada por *Physophora hydrostatica* con poblaciones extendidas al noroeste, oeste y sureste de las Islas Galápagos y recolectadas únicamente en arrastres oblicuos. (Fig. 27).

La familia *Agalmidae* presentaba *Agalma okeni* ampliamente distribuida por toda la región (Fig. 28), y *Stephanomia bijuga* se determinó en un arrastre oblicuo desde 369 m de profundidad.

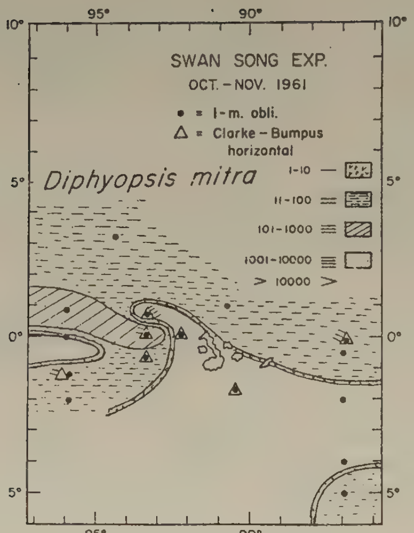
La familia *Pyrostephidae* incluye *Bargmannia elongata*, que se presentó solamente en la Estación 21, en arrastre oblicuo desde 277 m de profundidad.

Claramente se observa que en general, la mayor abundancia de especies y de poblaciones corresponden a las de régimen tropical.

La mayor parte de las especies de sifonóforos observadas en las colecciones de la Expedición SWAN SONG han sido previamente observadas por otros autores, según se puede comprobar en Alvariño (1971).

LOS CTENOFOROS DE LA REGION DE LAS ISLAS GALAPAGOS.

La única especie observada ha sido *Beroë forskali*, cuyas poblaciones son de régimen tropical, presentándose en arrastres oblicuos correspondientes a las Estaciones 9 y 21, respectivamente desde 448 m y 277 m de profundidad. Esta especie ha sido previamente determinada en esta región por Bigelow (1912).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SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Diphyopsis mitra
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11-100
101-1000
1001-10000
> 10000 >
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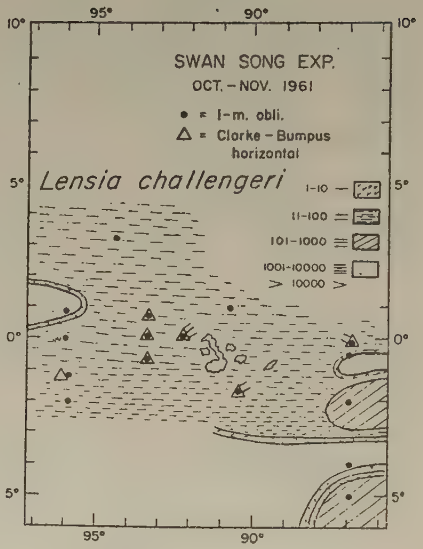
95°
90°

Fig. 22. Distribución de *Diphyopsis mitra* en la región de las Islas Galápagos.


95°
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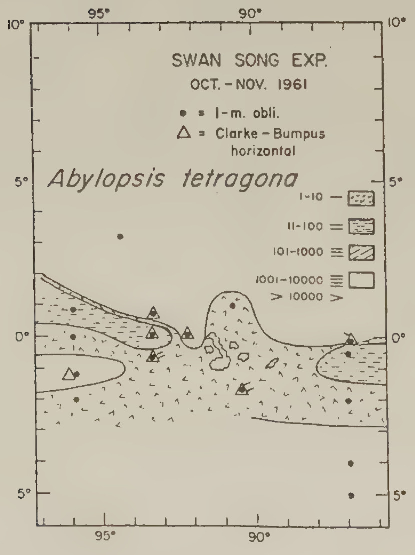
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Lensia challengeri
1-10
11-100
101-1000
1001-10000
> 10000 >
5°
5°
0°
0°
5°
5°
95°
90°

Fig. 23. Distribución de *Lensia challengeri* en la región de las Islas Galápagos.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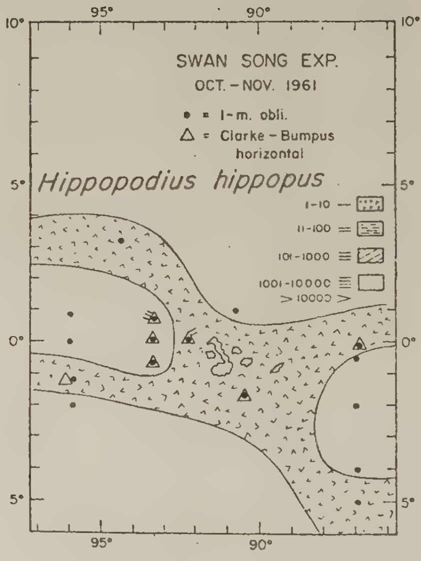
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Abylopsis tetragona
1-10
11-100
101-1000
1001-10000
> 10000 >
5°
5°
0°
0°
5°
5°
95°
90°

Fig. 24. Distribución de *Abylopsis tetragona* en la región de las Islas Galápagos.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SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Hippopodius hippopus
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11-100
101-1000
1001-10000
> 10000 >
5°
5°
0°
0°
5°
5°
95°
90°

Fig. 25. Distribución de *Hippopodius hippopus* en la región de las Islas Galápagos.

LAS MEDUSAS DE LA REGION DE LAS ISLAS GALAPAGOS.

Solamente se han obtenido 11 especies de medusas, cuatro para las colecciones procedentes de arrastres horizontales y la totalidad, excepto *Aglaura hemistoma*, se presentaban en los arrastres oblicuos.

Segura (1984) ha determinado 63 especies de medusas en la amplia región del Pacífico tropical oriental, sin embargo 4 especies encontradas en las colecciones de SWAN SONG no se observaron en material de Eastropac. Esta particularidad señala una vez más el fenómeno común a sifonóforos y medusas, grupos en los cuales la mayor parte de las especies presentan una distribución erratil (Alvariño 1977, Sears 1953) con poblaciones esparcidas en agregaciones irregulares, de aglomeración en ciertas localidades que quedan aisladas por amplias zonas oceánicas donde las especies están ausentes. En estos casos, el lance para capturar plancton tendría que coincidir con esas masivas agrupaciones. Además hay que considerar las características de los ciclos del desarrollo de las especies, velocidad de natación y estrato que habitan, sin olvidar que también son eficientes nadadores capaces de huir y evitar así ser capturados por las redes.

Como se ha indicado, la mayor parte de las especies determinadas corresponden con las mencionadas por Segura (1984), aunque *Solmissus marshalli*, *Cunina mucilaginosa*, *Phialidium malayense*, *Pelagia flaveola* se observaron en las colecciones de SWAN SONG pero no se encontraron en el material de Eastropac analizado por Segura. *Aglaura hemistoma* era la especie más abundante en las colecciones horizontales, seguida por *Rhopalonema velatum*, *Liriope tetraphylla* y *Pelagia noctiluca*. Esta última se encontró solamente en la Estación 11 a 35 m de profundidad. Sin embargo, *A. hemistoma* no se determinó en las colecciones de arrastres oblicuos.

Rhopalonema velatum era la más abundante en los arrastres oblicuos, seguida por *L. tetraphylla*. Estas dos especies son cosmopolitas, y las demás observadas en la región son de régimen tropical, aún cuando sus poblaciones eran escasas y diseminadas por toda la región. Se observa así una vez más la particularidad de la mayor parte de las especies de medusas, de presentarse en el plancton con carácter esporádico y errátil. Las especies más abundantes en la mayor parte del ámbito oceánico suelen ser generalmente las mismas que se han observado aquí más abundantes, y las demás especies mostraban una distribución errátil, tanto en localización espacial como en período de tiempo. Así, especies que se determinan en unas colecciones, no vuelven a encontrarse en otras muestras efectuadas en la misma región durante otro período de tiempo, aún cuando se trate de la misma estación climática.

Las Medusas son organismos que constituyen en algunos casos poblaciones meroplanctónicas, excepto las Narcomedusas y Traquimedusas que son holoplanctónicas. Sus poblaciones planctónicas se acumulan en ciertas localidades y épocas formando aglomeraciones de variada densidad, y los arrastres tendrían que coincidir precisamente en tiempo y localización con tales agrupaciones para que representantes de la especie se incluyeran en las colecciones (Tablas 6 y 7). La mayor parte de las especies encontradas en la zona de las Islas Galápagos son tropicales, y las más abundantes son las especies holoplanctónicas.

EL ORDEN LEPTOMEDUSAE.

La familia *Laodiceidae* está representada por *Toxorchis polynema* Kramp, especie tropical observada en la Estación 5 en arrastre oblicuo, y hay que añadir que esta especie no ha sido previamente señalada para el Océano Pacífico, pero Segura (1984) la ha observado en la zona del Pacífico tropical oriental.

La familia *Campanularidae* la representa *Phyalidium malayense* (Maas), en la Estación 21 (arrastre oblicuo).

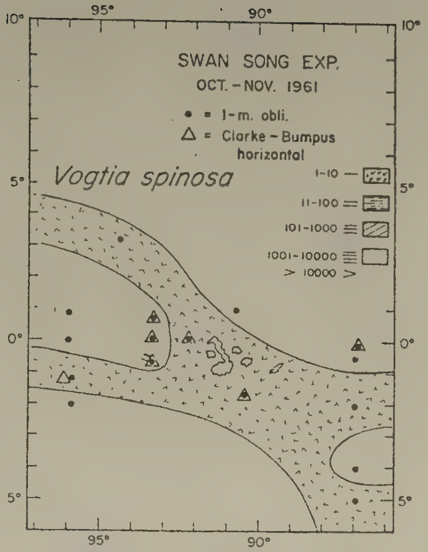
La familia *Aequoreidae* con *Aequorea macrodactyla* (Brandt) se ha encontrado en la Estación 22 (arrastre oblicuo). Se trata de una especie típical del Pacífico tropical y ha sido previamente determinada en esta región por Bigelow (1909), Kramp (1956), Segura (1984).

ORDEN TRACHYMEDUSAE.

La familia *Geryoniidae* incluye *Liriope tetraphylla* (Chamisso y Eysenhardt) especie cosmopolita observada también en el Pacífico tropical oriental (Segura 1984) y precisamente en la región de las Islas Galápagos (Vanhöffen 1913). (Fig. 29).

La familia *Rhopalonematidae* está representada por *Aglaura hemistoma* (Perón y Lesueur) (Fig. 30), y *Rhopalonema velatum* (Gegenbaur) (Fig. 31). Ambas especies han sido mencionadas previamente para la región por Vanhöffen (1913) y Segura (1984). La primera se presentaba aquí en los arrastres horizontales y *R. velatum* en ambas colecciones.

La familia *Aeginidae* con la especie tropical *Solmundella bitentaculata* (Quoy y Gaimard) se encontró en la Estación 21 (arrastre oblicuo), y ha sido anteriormente observada en el Pacífico oriental por Alvariño 1977, Kramp 1956, Segura 1984, Vanhöffen 1913.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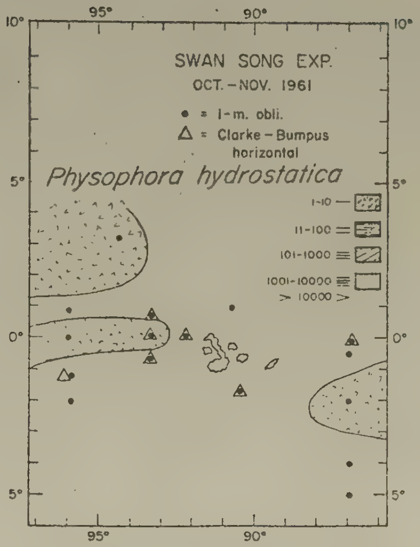
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Vogtia spinosa
1-10
11-100
101-1000
1001-10000
> 10000 >
95°
90°

Fig. 26. Distribución de *Vogtia spinosa* en la región de las Islas Galápagos.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SWAN SONG EXP.
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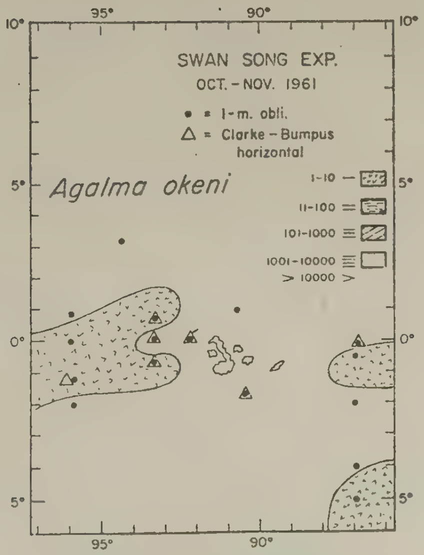
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Physophora hydrostatica
1-10
11-100
101-1000
1001-10000
> 10000 >
95°
90°

Fig. 27. Distribución de *Physophora hydrostatica* en la región de las Islas Galápagos.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SWAN SONG EXP.
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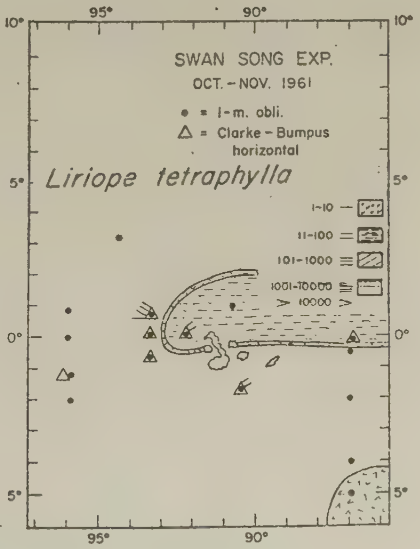
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Agalma okeni
1-10
11-100
101-1000
1001-10000
> 10000 >
95°
90°

Fig. 28. Distribución de *Agalma okeni* en la región de las Islas Galápagos.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90°
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5°
0°
5°
SWAN SONG EXP.
OCT. - NOV. 1961
● = 1-m. obli.
△ = Clarke - Bumpus horizontal
Liriope tetraphylla
1-10
11-100
101-1000
1001-10000
> 10000 >
95°
90°

Fig. 29. Distribución de *Liriope tetraphylla* en la región de las Islas Galápagos.

La familia *Cunínidae* incluye *Cunina mucilaginosa* (Chamisso y Eysenhardt), que se presentaba en la Estación 18 (arrastre oblicuo) y es la primera vez que esta especie ha sido determinada para el Pacífico tropical oriental. Además se observó *Solmissus marshalli* (Agassiz y Mayer) en la Estación 21 (Fig. 32), especie mencionada por Bigelow (1909, 1940) para la región.

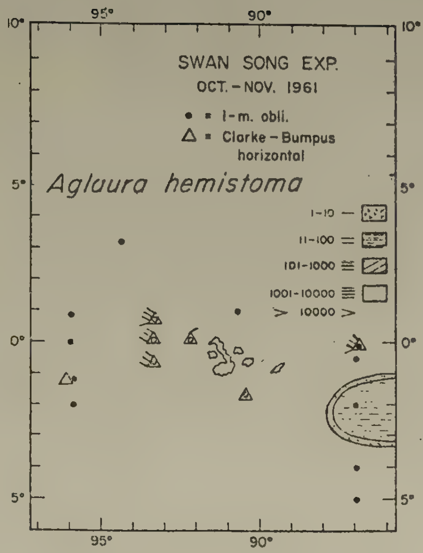
ORDEN SEMAEOSTOMEAE.

La familia *Pelagidae* incluye *Pelagia noctiluca* (Forskal) obtenida en la Estación 11 a 35 m de profundidad. Esta especie ha sido determinada por Bigelow (1928) para la región de las Islas Galápagos, y Segura (1984) para el Pacífico tropical oriental, en la zona de Costa Rica y Colombia (Bigelow 1940), y frente a Perú (Ranson 1945). *Pelagia flaveola* (Eschscholtz) se determinó en las Estaciones 11 y 27, y se trata de una medusa tropical que no ha sido previamente señalada para esta región ni zonas adyacentes.

La Estación 21 correspondiente a los arrastres oblicuos se caracteriza por la presencia de mayor número de medusas. Ahí concurren *R. velatum*, *L. tetraphylla*, *P. malayense*, *S. marshalli*, *S. bitentaculata*. En los arrastres horizontales, la Estación 11 incluía mayor número de especies de medusas, *R. velatum*, *L. tetraphylla*, *A. hemistoma*, *P. noctiluca*, pero la Estación 27 en arrastre horizontal incluye la mayor concentración de población en valores numéricos, aún cuando tales poblaciones estaban integradas solamente por las especies *R. velatum*, *L. tetraphylla*, *A. hemistoma*.

ALEVINES Y LARVAS OBTENIDOS DURANTE LA EXPEDICION SWAN SONG

Los alevines y larvas de peces que han sido observados en estas colecciones corresponden a treinta y una especies que se incluyen en por lo menos diez y siete familias. De ese total de especies, solamente once se han observado en las pescas horizontales y únicamente seis del total no aparecían en las colecciones procedentes de los arrastres oblicuos. Los *Leptocephalus* fueron separados de las colecciones antes de realizar este estudio y así no es posible determinar su notación específica ni genérica y solamente se señala la presencia de ejemplares en las muestras correspondientes, adjudicándoles la denominación general de *Leptocephalus*. Por esta razón se ha decidido que en las determinaciones de alevines y larvas de peces no se incluyeran valores cuantitativos para cada una de las especies, indicándose la presencia de las respectivas especies.


95°
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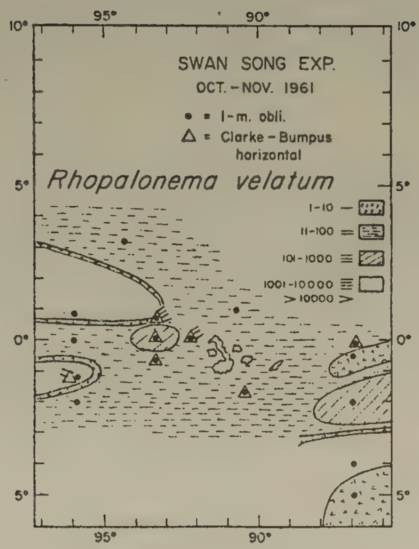
SWAN SONG EXP.
OCT. - NOV. 1961
● = I-m. obli.
△ = Clarke - Bumpus horizontal
5°
Aglaura hemistoma
1-10 —
11-100 =
101-1000 ≡
1001-10000 ≣
> 10000 >
0°
5°

Fig. 30. Distribución de *Aglaura hemistoma* en la región de las Islas Galápagos.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SWAN SONG EXP.
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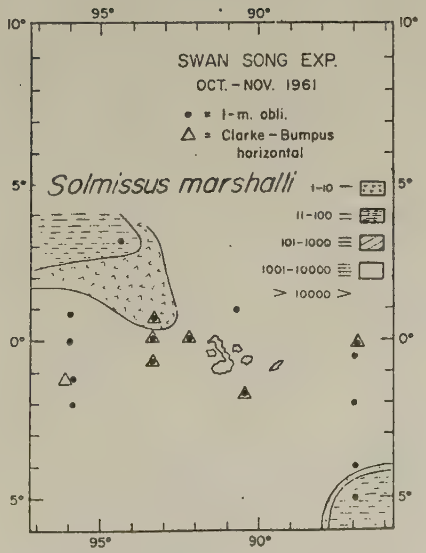
● = I-m. obli.
△ = Clarke - Bumpus horizontal
5°
Rhopalonema velatum
1-10 —
11-100 =
101-1000 ≡
1001-10000 ≣
> 10000 >
0°
5°

Fig. 31. Distribución de *Rhopalonema velatum* en la región de las Islas Galápagos.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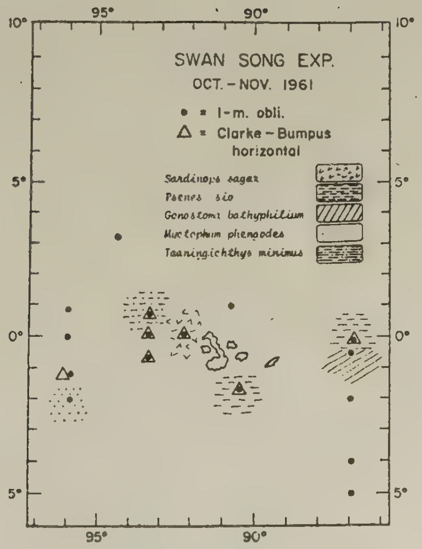
SWAN SONG EXP.
OCT. - NOV. 1961
● = I-m. obli.
△ = Clarke - Bumpus horizontal
5°
Solmissus marshalli
1-10 —
11-100 =
101-1000 ≡
1001-10000 ≣
> 10000 >
0°
5°

Fig. 32. Distribución de *Solmissus marshalli* en la región de las Islas Galápagos.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SWAN SONG EXP.
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● = I-m. obli.
△ = Clarke - Bumpus horizontal
5°
Sardinops sagax
Psenes sio
Gonostoma bathyphilium
Myctophum phengodes
Taaningichthys minimus
0°
5°

Fig. 33. Distribución de las larvas de peces en la región de las Islas Galápagos: *Psenes sio*, *Gonostoma bathyphilium*, *Myctophum phengodes*, *Taaningichthys minimus*, *Sardinops sagax*.

Como puede observarse en las Tablas 8 y 9, las larvas y estados juveniles de los peces aparecen diseminados por toda la región investigada, restringiendo su distribución principalmente a la zona alrededor de las islas y ausentándose de las localidades más alejadas al norte, oeste y suroeste del archipiélago.

Las especies más frecuentes en las pescas oblicuas, *Lampanyctus idostigma*, *Cyclothone acclinidens* se obtuvieron en cuatro localidades, respectivamente en las Estaciones 18, 20, 22, 27 y Estaciones 9, 14, 22, 29. Especies que se presentaban solamente en tres localidades, *Benthosema panamensis*, *Vinciguerria lucetia*, y las demás especies se encontraron solamente en una o dos localidades.

Familia *Clupeidae*.- Se han obtenido larvas de *Sardinops sagax* (Jenyns) en la Estación 11 a 35 m de profundidad. (Fig. 33).

Familia *Nomeidae*.- Larvas de *Psenes sio* Haedrich, han sido observadas en las Estaciones 14 y 22 de las colecciones obtenidas en arrastres horizontales, respectivamente a 20 m y 70 m de profundidad. (Fig. 33).

Familia *Carangidae*.- *Naucrates ductor* (L.) se presentaba en la Estación 27 a 10 m de profundidad (Fig. 34).

Familia *Myctophidae*.- En este estudio *Myctophum nitidulum* Ahlstrom se observó en la Estación 22 a 3 m de profundidad y en el arrastre oblicuo de la Estación 4, mientras que *M. phengodes* (Lutken) ocurría en la Estación 7, (Figs. 33 y 34). *Taaningihthys minimus* (Taning) se encontró en la Estación 27, (Fig. 33). *Diogenychthys laternatus* (Garman) se determinó en las Estaciones 21 y 23 y en la Estación 8 en un arrastre a 11 m de profundidad, (Fig. 35). *Benthosema panamensis* (Taning) se encontró en las Estaciones 16, 22, 25 en arrastres oblicuos respectivamente desde 245, 318 y 238 m de profundidad, (Fig. 36). *Gonichthys termiculus* (Garman) solamente se observó en la Estación 3, en un arrastre desde 448 m de profundidad hasta la superficie oceánica (Fig. 37). Larvas de *Diaphus* sp. se determinaron en la Estación 7, Fig. 35 *Lampanyctus idostigma* Parr estaba representado en las Estaciones 18, 20, 22, 27, en arrastres oblicuos respectivamente desde 190 m, 218 m, 318 m, de profundidad (Fig. 38).

Familia *Bathylagidae*. Ejemplares de *Bathylagus nigrigenys* Parr se observaron en la Estación 18, en un arrastre desde 190 m y en la Estación 14 en la pesca horizontal efectuada a 75 m de profundidad, (Fig. 34). *Leuroglossus stilbius* Gilbert, *B. pacificus* Gilbert, se encontraron solamente en las colecciones de arrastres horizontales, respectivamente en las Estaciones 27 y 11, en profundidades de 10 m (Figs. 34 y 35).

Familia *Gonostomatidae*.- *Cyclothone acclinidens* Garman estaba en las Estaciones 9, 14, 22, 27, en arrastres efectuados respectivamente desde 448, 350, 318, 301 m de profundidad (Fig. 35). *C. braueri* Jespersen y Taning, en un arrastre oblícuo desde 139 m (Fig. 38). *Gonostoma bathyphilium* (Vaillant) se observó en la Estación 16, en arrastres desde 245 m de profundidad (Fig. 33). *Vinciguerria lucetia* (Garman) se observó en el arrastre horizontal a 35 m de profundidad en la Estación 11 y en arrastres oblicuos en las Estaciones 7, 16, 18 (Fig. 37).

Familia *Sternoptychidae* incluía alevines de *Argyropelecus hawaiensis* Schultz y *A. lychnus* Garman, (Baird, 1971) observados respectivamente en las Estaciones 4 y 24, (Figs. 36 y 37).

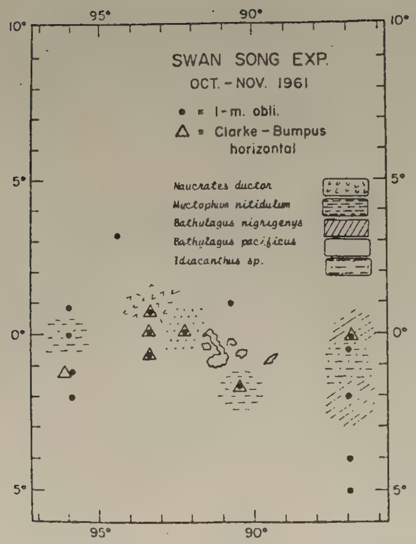
Familia *Idiacanthidae*.- Larvas de *Idiacanthus* sp. se encontraron en el arrastre desde 245 m de profundidad en la Estación 16 (Fig. 34).

Familia *Moridae*.- Larvas de *Physiculus* sp. han sido observadas en el arrastre desde 318 m de profundidad en la Estación 27 (Fig. 36).

Familia *Cynoglossidae*.- Larvas de *Symphurus atricauda* (Jordan y Gilbert) se determinaron en la Estación 5, en pescas desde 277 m de profundidad. (Fig. 36).

Familia *Antennariidae*.- Larvas correspondientes a especies de esta familia se obtuvieron en la Estación 14, desde 350 m de profundidad (Fig. 36).

Familia *Ogcocephalidae*.- Un alevín de unos 23 mm de longitud encontrado en la Estación 16, debe posiblemente adjudicarse a esta familia (Fig. 36). El ejemplar se ha separado de la muestra de plancton con objeto de tenerlo disponible para cuando se consigan otros y poder preparar la serie completa de sus fases de desarrollo larval y juvenil, con el fin de determinar la especie (Fig. 39). En esta región se han determinado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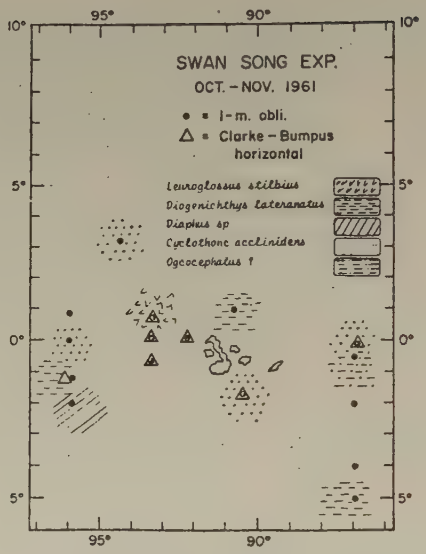
SWAN SONG EXP.
OCT. - NOV. 1961
● = I-m. obli.
△ = Clarke - Bumpus horizontal
Naucrates ductor
Myctophum nitidulum
Bathylagus nigrigenys
Bathylagus pacificus
Idiacanthus sp.

Fig. 34. Distribución de las larvas de peces en la región de las Islas Galápagos: *Naucrates ductor*, *Myctophum nitidulum*, *Bathylagus nigrigenys*, *Bathylagus pacificus*, *Idiacanthus sp.*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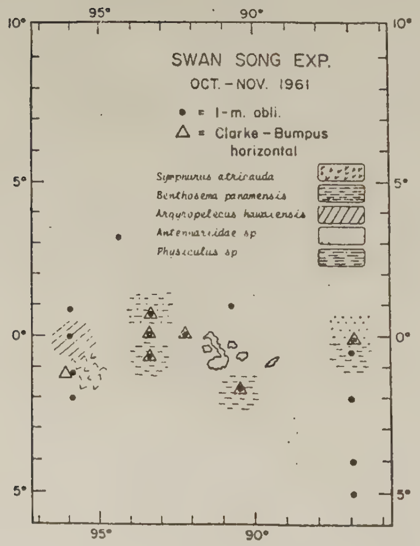
SWAN SONG EXP.
OCT. - NOV. 1961
● = I-m. obli.
△ = Clarke - Bumpus horizontal
Leuroglossus stilbius
Diogenichthys lateranatus
Diaphus sp
Cyclothone acclinidens
Ogcocephalus ?

Fig. 35. Distribución de las larvas de peces en la región de las Islas Galápagos: *Leuroglossus stilbius*, *Diogenichthys laternatus*, *Diaphus sp.*, *Cyclothone acclinidens*, *Agcocephalus ?*.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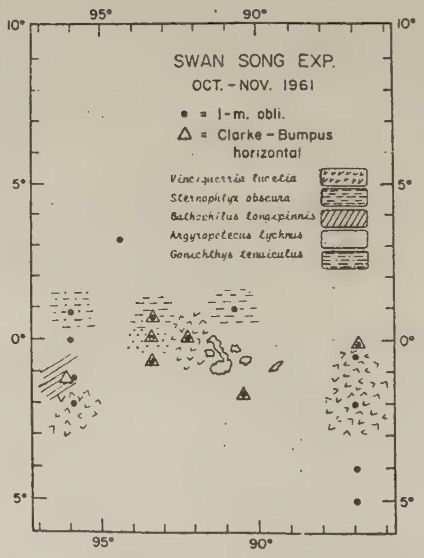
5°
0°
5°
SWAN SONG EXP.
OCT. - NOV. 1961
● = I-m. obli.
△ = Clarke - Bumpus horizontal
Symphurus atricauda
Benthosema panamensis
Argyropelecus hawaiensis
Antennariidae sp
Physiculus sp

Fig. 36. Distribución de las larvas de peces en la región de las Islas Galápagos: *Symphurus atricauda*, *Benthosema panamensis*, *Argyropelecus hawaiensis*, *Antennariidae sp.*, *Physiculus sp.*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SWAN SONG EXP.
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● = I-m. obli.
△ = Clarke - Bumpus horizontal
Vinciguerria lucetia
Sternoptyx obscura
Bathophilus longipinnis
Argyropelecus lychnus
Gonichthys tenuiculus

Fig. 37. Distribución de las larvas de peces en la región de las Islas Galápagos: *Vinciguerria lucetia*, *Sternoptyx obscura*, *Bathophilus longipinnis*, *Argyropelecus lychnus*, *Gonichthys tenuiculus*.

los adultos de *Ogcocephalus darwini* Hubbs, y en otras zonas *O. porrectus* y *Zalieutes elater* (Hubbs 1958).

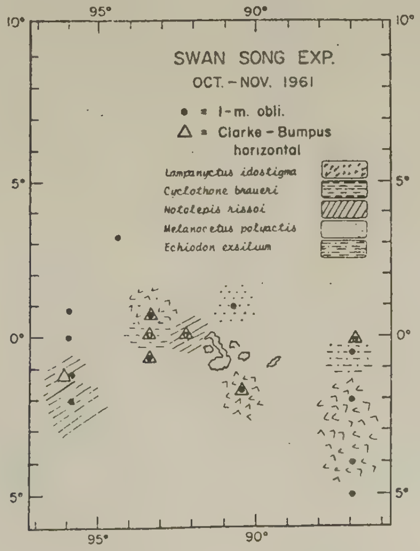
Familia *Melanostomiatidae*.- Se presentó únicamente *Bathopylus longipinnis* (Pappenheim), en la Estación 8, en un arrastre a 11 m de profundidad (Fig. 37).

Familia *Paralepididae*.- Larvas de *Notolepis rissoi* (Bonaparte) se identificaron en las colecciones de las Estaciones 8 y 11 en arrastres a 42 m y 10 m de profundidad, respectivamente, y en la Estación 7 en un arrastre oblicuo desde 329 m de profundidad (Fig. 38).

Familia *Melanocetidae*.- Se han observado larvas de *Melanocetus polydactis* Regan en la Estación 23 (Fig. 38).

Familia *Carapidae*.- Está representada por *Echiodon exsilium* Rosenblatt, en la Estación 16, en un arrastre desde 245 m de profundidad (Fig. 38).

Los *Leptocephalus* se distribuían en las colecciones procedentes de los arrastres oblicuos, con 2 ejemplares en la ESTACION 3 y uno en la Estación 16.


95°
90°
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10°
SWAN SONG EXP.
OCT. – NOV. 1961
● = 1-m. obli.
△ = Clarke – Bumpus horizontal
Lampanyctus idostigma
Cyclothone braueri
Notolepis rissoi
Melanocetus polyactis
Echiodon exsilium
5°
5°
0°
0°
5°
5°
95°
90°

Fig. 38. Distribución de las larvas de peces en la región de las Islas Galápagos: *Lampanyctus idostigma, Cyclothone braueri, Notolepis rissoi, Meleanocetus polyactis, Echiodon exsilium.*

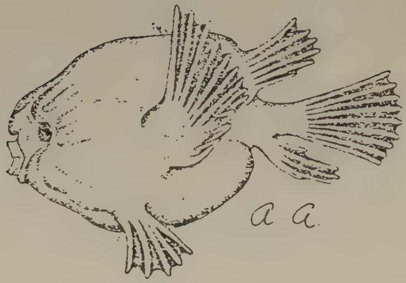

Fig. 39. Alevin de *Ogcocephalus*.

TABLA 1. DATOS DE LA EXPEDICION SWAN SONG EN LA REGION DE LAS ISLAS GALAPAGOS.

Arrastres horizontales con red Clarke-Bumps

Estación	Fecha	Hora local	Posición	Profundidad en m
B-8	25 octubre 1961	1734-1804	01°08'S-95°58'W	11
B-8	25 octubre 1961	1734-1804	01°08'S-95°58'W	42
B-11	28 octubre 1961	0639-0709	00°04'N-92°16'W	10
B-11	28 octubre 1961	0639-0709	00°04'N-92°16'W	35
B-11	28 octubre 1961	0639-0709	00°04'N-92°16'W	100
B-14	3 noviembre 1961	1520-1550	00°08'S-86°55'W	20
B-14	3 noviembre 1961	1520-1550	00°08'S-86°55'W	75
B-22	16 noviembre 1961	1845-1920	01°43'S-90°29'W	3
B-22	16 noviembre 1961	1845-1920	01°43'S-90°29'W	15
B-22	16 noviembre 1961	1845-1920	01°43'S-90°29'W	70
B-24	20 noviembre 1961	0442-0512	00°04'N-93°24'W	10
B-24	20 noviembre 1961	0442-0512	00°04'N-93°24'W	55
B-25	20 noviembre 1961	2038-2108	00°04'S-93°24'W	55
B-25	20 noviembre 1961	2038-2108	00°04'S-93°24'W	160
B-27	21 noviembre 1961	2019-2049	00°44'N-93°20'W	10
B-27	21 noviembre 1961	2019-2049	00°44'N-93°20'W	55

Arrastres oblicuos con red de 1 m de diámetro

Estación	Fecha	Hora local	Posición	Profundidad en m
B-3	20 octubre 1961	0449-0520	00°52'N-95°56'W	448
B-4	21 octubre 1961	0432-0503	00°02'S-96°02'W	386
B-5	22 octubre 1961	0905-0929	01°09'S-95°59'W	277
B-8	24 octubre 1961	2109-2137	02°00'S-95°56'W	329
B-9	26 octubre 1961	0611-0642	00°02'S-96°01'W	448
B-11	28 octubre 1961	0455-0524	00°04'N-92°16'W	355
B-13	2 noviembre 1961	0550-0618	00°08'S-86°55'W	190
B-14	3 noviembre 1961	1250-1320	00°08'S-86°55'W	350
B-16	6 noviembre 1961	0346-0416	00°30'S-86°58'W	245
B-18	7 noviembre 1961	2322-2351	02°01'S-87°02'W	190
B-20	8 noviembre 1961	1454-1530	04°00'S-87°00'W	218
B-21	8 noviembre 1961	2124-2152	05°01'S-86°59'W	277
B-22	16 noviembre 1961	0748-0822	01°43'S-90°29'W	318
B-23	18 noviembre 1961	1659-1729	01°00'N-90°45'W	369
B-24	20 noviembre 1961	0331-0409	00°04'N-93°24'W	139
B-25	20 noviembre 1961	1935-2010	00°40'S-93°24'W	238
B-27	21 noviembre 1961	1854-1939	00°44'N-93°20'W	318
B-29	24 noviembre 1961	1232-1305	03°13'N-94°23'W	301

TABLA 2. ABUNDANCIA DE QUETOGNATOS EN PESCAS HORIZONTALES.
EXPEDICION SWAN SONG
(* Sin datos sobre el agua filtrada durante el arrastre)

Estaciones	8	8	11	11	11	14	14	22	22	22	24	24	25	25	27	27	Total	Frecuencia %
Profundidad	11 m	42 m	10 m	35 m	100m	20 m	75 m	3 m	15 m	70 m	10 m	55 m	55 m	160m	10 m	55 m		
Especies																		
Eukrohnia hamata																		
Krohnitta pacifica	581						72	44	100	153	11		1*		1285	166	2413	56
Krohnitta subtilis		75					54	89	200	307		1*					726	37
Pterosagitta draco	348	50	560			14000			200		22		1*		33142	1333	49656	56
Heterokrohnia mirabilis														125			125	6
Sagitta bedoti	581		186	27		416	72	179		153		1*				166	17801	56
Sagitta bierii		350	2160	27		1250	144		400	153			1*	250		1333	6067	62
Sagitta bipunctata															1000		1000	6
Sagitta decipiens		25	93	55	66		163	44									446	37
Sagitta enflata	1860	25	2480	27		46666	18	890	5600	923	22	1*	19*	625	65714	3000	127870	94
Sagitta ferox																		
Sagitta hexaptera	744	1425	560	13	66				100	153	11	1*	2*	125	1000	166	4366	81
Sagitta maxima																		
Sagitta minima	232	50							200		11			125		1000	1618	37
Sagitta neglecta																		
Sagitta pacifica	465		93	333	22	3333			100	153	45	1*	1*	250	11000		15796	75
Sagitta pulchra	232					416		268							2000		2916	19
Sagitta robusta																		
Sagitta zetesios																		

TABLA 3. ABUNDANCIA DE LOS QUETOGNATOS EN LAS PESCAS OBLICUAS
EXPEDICION SWAN SONG

Estaciones	3	4	5	7	9	11	13	14	16	18	20	21	22	23	24	25	27	29	Total	Frecuencia %
Profundidad	448m	386m	277m	329m	448m	355m	190m	350m	245m	190m	218m	277m	318m	369m	139m	238m	318m	301m		
Especies																				
Eukrohnia hamata					12							16							28	11
Krohnitta pacifica								35				101	19						155	17
Krohnitta subtilis	23						28	123	61	23	14		76	31	39			23	441	55
Pterosagitta draco	51			12		66	144	200	58	34	17	81		39	89		112	38	941	72
Heterokrohnia mirabilis																				
Sagitta bedoti	102	175	125			106	183	235	237	514	300	119	80	78	287	40	282	43	2906	89
Sagitta bierii		67		253	457	45	57						153		125	34		166	1357	50
Sagitta bipunctata																				
Sagitta decipiens		40	38	41	15	45	14							93	124	36	8	14	468	61
Sagitta enflata	282	90	322	27	60	27	614	735	508	1201	112	245	1500	990	424	17	247	66	7467	100
Sagitta ferox		45					34				12							89	180	22
Sagitta hexaptera	230	141	274	55	84	42	65	205	125	160	20	32	115	50	165	63	44	64	1934	100
Sagitta maxima	5	10	9	6	19	21		29	48	20							11	15	193	61
Sagitta minima	25										14	16							55	17
Sagitta neglecta							14	76	22		91		57						260	28
Sagitta pacifica	258			60			185	176	169		118	229	19	21	215		176	341	1967	67
Sagitta pulchra							197	58	69	66				40					453	33
Sagitta robusta														43					43	5
Sagitta zetesios	15																		15	5

TABLA 4. ABUNDANCIA DE SIFONOFOROS EN LAS PESCAS HORIZONTALES
EXPEDICION SWAN SONG
(* Sin datos sobre el agua filtrada durante el arrastre)

Estaciones	8	8	11	11	11	14	14	22	22	22	24	24	25	25	27	27	Total	Frecuencia %
Profundidad	11m	42m	10m	35m	100m	20m	75m	3m	15m	70m	10m	55m	55m	160m	10m	55m		
Especies																		
Muggiaea kochi	11	225	186	194					300				4*	125	3714	666	5425	56
Chelophyes appendiculata		75	93	13			18		100		22				4000		4621	44
Chelophyes contorta															7521		7571	6
Diphyes bojani	11												1*				12	12
Diphyes bojani (eudoxias)																166	166	6
Diphyes dispar	11																11	6
Diphyopsis mitra		25									22				3428	166	3641	25
Diphyopsis mitra (eudoxias)							355				11						366	12
Lensia campanella		25															25	6
Lensia challengeri					266		109			153							528	19
Lensia hotspur																		
Sulculeolaria bigelowi				13													13	6
Sulculeolaria monoica																		
Sulculeolaria turgida																		
Sulculeolaria quadrivalvis																		
Abylopsis eschscholtzi																		
Abylopsis tetragona							18			75				125			219	19
Ceratocymba sagittata																		
Hippopodius hippopus				41											571		612	12
Vogtia kuruae														250			250	6
Vogtia spinosa																		
Rosacea cymbiformis					177												177	6
Amphicaryon ernesti																		
Nectodroma reticulata																		
Phusophora hydrostatica																		
Agalma okeni					22												22	6
Stephanomia bijuga																		
Bargmannia elongata																		

TABLA 5. ABUNDANCIA DE SIFONOFOROS EN LAS PESCAS OBLICUAS . EXPEDICION SWAN SONG

Estaciones Profundidad Especies	3 448m	4 386m	5 277m	7 329m	9 448m	11 355m	13 190m	14 360m	16 245m	18 190m	20 218m	21 277m	22 318m	23 369m	24 139m	25 238m	27 318m	29 301m	Total	Frecuencia %
Muggiaea kochi	25			24	15				16										80	22
Chelophyes appendiculata	51	29	16	12	47							19			124	62	14	12	386	55
Chelophyes contorta	25							29		32				53				47	186	28
Diphyes bojani																				
Diphyes dispar		4			11				11										26	17
Diphyopsis mitra	390		16	18			48	32	56			88		28	129	30		23	858	61
Lensia campanella																				
Lensia challengeri		31	16	31	15	51	95			224		136	115	37	43	65	34	50	943	78
Lensia hotspur										21									21	5
Sulculeolaria bigelowi																		28	28	5
Sulculeolaria monoica								14											14	5
Sulculeolaria turgida	51			10															61	11
Sulculeolaria quadrivalvis																		11	11	5
Abylopsis eschscholtzi					3														3	5
Abylopsis tetragona	25	8		5	9				11	4			5	4	13	7			91	55
Abylopsis tetragona (eudoxias)				9												15			24	11
Ceratocymba sagittata			1																1	5
Hippopodius hippopus			1			4		1				6	3					1	16	33
Vogtia kuruae									3										3	5
Vogtia spinosa			1			3				8		3	3					1	19	33
Rosacea cymbiformis																				
Amphicaryon ernesti				5															5	5
Nectodroma reticulata																		1	1	5
Physophora hydrostatica		1								6					2			1	10	22
Agalma okeni			1		1							2				1	1		7	33
Stephanomia bijuga														1					1	5
Bargmannia elongata												2							2	5

TABLA 6. ABUNDANCIA DE MEDUSAS EN PESCAS HORIZONTALES, EXPEDICION SWAN SONG
(* Sin datos sobre el agua filtrada durante el arrastre)

Estaciones Profundidad Especie	8 11m	8 42m	11 10m	11 35m	11 100m	14 20m	14 75m	22 3m	22 15m	22 70m	24 10m	24 55m	25 55m	25 160m	27 10m	27 55m	Total	Frecuencia %
Rhopalonema velatum		150	93	27	422								3*		7000	500	8195	44
Liriope tetraphylla				55				100							1714	166	2035	25
Aglaura hemistoma				27		1250					18	3*	4*	250	8428	500	10380	50
Phialidium malayense																		
Solmissus marshalli																		
Solmundella bitentaculata																		
Aequorea macrodactyla																		
Toxorchis polynema																		
Pelagia noctiluca				13														
Pelagia flaveola																	13	6

TABLA 7. ABUNDANCIA DE MEDUSAS EN LAS PESCAS OBLICUAS. EXPEDICION SWAN SONG.

Especie Profundidad Especie	3 448m	4 386m	5 277m	7 329m	9 448m	11 355m	13 190m	14 350m	16 245m	18 190m	20 218m	21 277m	22 318m	23 369m	24 139m	25 238m	27 318m	29 301m	Total	Frecuencia %
Rhopalonema velatum		60		48		30	32	20	12	481		9	34	70	248	58		51	1153	72
Liriope tetraphylla						12		14				6		26					58	22
Aglaura hemistoma																				
Phialidium malayense												6							6	5
Solmissus marshalli												14					5	12	31	17
Solmundella bitentaculata												19							19	5
Aequorea macrodactila													11						11	5
Cunina mucilaginosa										2									2	5
Toxorchis polynema			1																1	5
Pelagia noctiluca															2				2	5
Pelagia flaveola						9											3		12	11

TABLA 8. ALEVINES Y LARVAS DE PECES EN ARRASTRES HORIZONTALES. EXPEDICION SWAN SONG.

Estaciones	8	8	11	11	11	14	14	22	22	22	24	24	25	25	27	27	Frecuencia %
Profundidad	11m	42m	10m	35m	100m	20m	75m	3m	15m	70m	10m	55m	55m	150m	10m	55m	
Especies																	
Sardinops sagax				x													6
Psenes sio						x				x							12
Naucrates ductor															x		6
Myctophum nitidulum								x									6
Myctophum phenaodes																	
Lampanyctus idostigma																	
Leurogrossus stilbius															x		6
Bathylagus nigrigenus							x										6
Bathylagus pacificus			x														6
Bathopulus longipinnis	x																6
Gonostoma bathyphylium																	
Gonichthus termiculus																	
Cyclothone acclinidens																	
Cyclothone braueri																	
Notolepis rissoi		x	x														12
Diogenichthys laternatus	x																6
Melanocetus polyactis																	
Echiodon exsilium																	
Symphorus atricauda																	
Benthosema panamensis																	
Argyropelecus hawaiensis																	
Argyropelecus lychnus																	
Sternoptys obscura																	
Taaningichthys minimus																	
Vincigierria lucetia				x													6
Diaphus sp.																	
Antenariidae sp.																	
Physiculus sp.																	
Idiacanthys sp.																	
Ogcocephalus sp.																	
Leptocephalus spp.																	

TABLA 9. ALEVINES Y LARVAS DE PECES EN ARRASTRES OBLICUOS. EXPEDICION SWAN SONG.

Estaciones Profundidad Especies	3 448m	4 386m	5 277m	7 329m	9 448m	11 355m	13 190m	14 350m	16 245m	18 190m	20 218m	21 277m	22 318m	23 369m	24 139m	25 238m	27 318m	29 301m	Frecuencia %
Sardinops sagax																			
Psenes sio																			
Naucrates ductor																			
Myctophum nitidulum		x																	5
Myctophum phengodes				x															5
Lampanyctus idostigma										x	x		x				x		22
Leuroglossus stilbius																			
Bathylagus nigrigenus										x									5
Bathylagus pacificus																			
Bathophilus longipinnis																			
Gonostoma bathyphyllium									x										5
Gonichthys termiculus	x																		5
Cyclothone acclinidens					x			x					x					x	22
Cyclothone braueri															x				5
Notolepis rissoi				x															5
Diogenichthys laternatus												x		x					11
Melanocetus polyactis														x					5
Echiodon exsilium									x										5
Symphurus atricauda			x																5
Benthosema panamensis									x				x			x			17
Argyropelecus hawaiiensis		x																	5
Argyropelecus lychnus															x				5
Sternoptyx obscura														x			x		11
Taaningichthys minima																	x		5
Vinciguerria lucetia				x					x	x									17
Diaphus sp.				x															5
Antennariidae sp.								x											5
Physiculus sp.																	x		5
Idiacanthus sp.									x										5
Ogcocephalus sp.									x										5
Leptocephalus spps.	x								x										11

CONCLUSIONES

Amplias zonas de surgencia se señalan al este y oeste de las islas, identificadas mediante los perfiles hidrográficos y la distribución de las especies indicadoras del plancton.

El año 1961 ha sido de régimen normal. En la zona de las Islas Galápagos se altera la dinámica oceánica con el fenómeno de "El Niño". El período de esta Expedición coincide justamente entre dos períodos en que se desarrolló un fuerte fenómeno de "El Niño", 1958 y 1965.

Puede representarse la extensión e influencia de las aguas tropicales por la distribución de las especies típicas de las mismas, principalmente los Quetognatos *Krohnitta pacifica*, *Sagitta bedoti*, *S. neglecta*, *S. ferox*, *S. pulchra*, *S. robusta*, añadiendo *S. regularis*, *S. popovicii*, *S. peruviana* (aunque estas tres últimas no se encontraron en las colecciones de la Expedición SWAN SONG); los Sifonóforos *Chelophyes contorta*, *Diphyopsis mitra*, *Abylopsis eschscholtzi*, *A. tetragona*, *Muggiaea kochi*, *Ceratocymba sagittata*, y otros *Abylinae* (aunque no se han determinado en estas colecciones); así como las Medusas *Aglaura hemistoma*, *Solmundella bitentaculata* y otras especies características.

La mayor parte de las larvas de peces determinadas corresponden a especies tropicales.

La abundancia de larvas de peces se ha observado preferentemente alrededor de las islas. Ahí los remolinos mantienen la población en el sistema virtualmente cerrado, aunque recibe aportes con los que fluye alimento, que nutren la persistencia del sistema y de las poblaciones que lo integran.

La mayor abundancia de larvas de peces se obtuvo en la Estación 16 de las colecciones mediante arrastres oblicuos, coincidiendo en esa localidad con 9 especies de Quetognatos, la mayor parte tropicales, 5 especies de Sifonóforos y la medusa *Rhopalonema velatum*. La falta de datos sobre valores numéricos para las larvas no permite desarrollar un análisis entre el plancton e ictioplancton como en Alvariño (1980).

Sardinops sagax coincidía en su distribución con *Bathylagos pacificus*, *Vinciguerria lucetia* y con la mayor parte de los Quetognatos y todas las medusas en los arrastres horizontales, así como 7 especies de Sifonóforos.

No se han determinado larvas de peces en los arrastres a 55 m de profundidad, en uno a 15 m, 100 y 150 m de profundidad, y solamente en dos arrastres oblicuos no se observaron larvas.

Las larvas y juveniles de peces mencionados, han sido previamente observadas en esta región de las Islas Galápagos y zonas adyacentes (Ahlstrom 1971, 1972; Ahlstrom y Counts 1958; Ahlstrom y Moser 1969, Ahlstrom, Butler y Sumida 1976; Alverson 1961; Garman 1899; Grey 1960; Haedrich 1966; Hildebrand 1946; Horn y Haedrich 1973; Morrow 1957; Parin 1968; Wisner 1971, 1977) exceptuando *Myctophum phengodes*, *Taaningiehthys minimus*, *Bathylagus pacificus*, *Cyclothone acclinidens*, *C. braueri*, *Gonostoma bathyphilium*, *Argyropelecus hawaiensis*, *Physiculus* sp., *Ogcocephalidae* sp., *Bathophylus longipinnis*, *Notolepis rissoi*, *Echiodon exsilium*.

CONCENTRACION DE LAS ESPECIES EN RELACION CON LA HORA DE ARRASTRE.

Los Quetognatos presentaban mayor número de especies congregadas en la Estación 13, a las 0550-0618 horas, seguida por los Estaciones 14 y 29, respectivamente a las 1250-1320 y 1230-1305 horas. En estas Estaciones concurrían diez especies de Quetognatos, y las Estaciones 3, 16, 12, 22, 23 incluían nueve especies cada una, de las cuales las dos primeras Estaciones correspondían al período nocturno. Los Sifonóforos eran más abundantes en la Estación 29, en arrastres efectuados a las 1232-1305 horas. Las medusas señalaban una concentración mayor de especies en la Estación 21, donde concurrían cinco especies, y el arrastre pertenecía a horas de la noche.

En los diez arrastres diurnos horizontales, dos de ellos no contenían larvas de peces. Sin embargo, en los seis arrastres efectuados de noche, solamente uno resultó positivo para larvas y alevines de peces. Las colecciones correspondientes a los arrastres oblicuos, diez se efectuaron durante el día y ocho en la noche, resultando con una estación diurna y otra nocturna sin larvas de peces. La mayor concentración de especies de peces, considerado sus larvas y alevines respectivos, se presentaban en la Estación 16 efectuada a las 03:46 horas, desde 245 m de profundidad.

Todos estos datos indican que el período del día no afecta notablemente los resultados en relación con la distribución cualitativa y cuantitativa de las especies correspondientes a los grupos estudiados en esta serie de muestras. Sin embargo, para establecer resultados categóricos sobre este problema, sería preciso un estudio detallado de la región, mediante arrastres a varios estratos de profundidad y a diversas horas del día y de la noche, utilizando redes de apertura y cierre automáticos. De esa forma se podrían determinar las variaciones que se presentan en la distribución batimétrica de las especies en relación con el factor iluminación. Alverson (1961) indica que la presencia de Mictofidos en las muestras de plancton está relacionada con la hora de arrastre. Pero, en las colecciones estudiadas, Mictofidos se presentaban en las muestras obtenidas durante el día y la noche.

Un plan continuo de estudios sobre el plancton de esta región y zonas adyacentes, serviría para determinar las bases de las características, variaciones y alteraciones en las poblaciones, que indicarían la situación de la dinámica oceánica de la región, a lo largo de los años y sus estaciones climáticas. La información obtenida proporcionaría la clave para pronosticar variaciones en el sistema, determinar la iniciación, evolución, desarrollo inminente y pleno, alteraciones y efectos que se desencadenan y constituyen el fenómeno bien conocido de El Niño. Es evidente, que planes similares son recomendables y aplicables a todas las regiones oceánicas, proporcionando así acopio de conocimientos básicos sobre el sistema marino y sus poblaciones.

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8604

The Occurrence of Young Skipjack Tuna (*Katsuwonus pelamis*) in the Diet of Adult Skipjack from the Southwestern Atlantic Ocean

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Stomach contents of skipjack tuna captured in 1981–1982 by pole-and-line gear off the southern coast of Brazil were analyzed for the presence of larval and juvenile skipjack. The percent frequency of occurrence, percent number and percent volume were evaluated, Of the 1041 stomachs that were examined for food, 436 were empty. The mean volume of food in all stomachs analyzed was 36.9 ml, of which 18.9 ml was bait and 18.0 ml was prey. Larval and juvenile skipjack were not present in the diet of adults from this study.

Les contenus stomacaux de listaos capturés en 1981–82 à la canne au large des côtes sud du Brésil ont été analysés à la recherche de stades larvaires et juvéniles de l'espèce. Le degré de fréquence et les pourcentages numérique et de volume ont été calculés. Sur les 1041 estomacs dont le contenu alimentaire a été étudié, 436 étaient vides. La quantité moyenne de nourriture pour tous les estomacs étudiés était 36,9 ml, dont 18,9 d'appât et 18,0 d'espèces-proies. Aucun listao des stades juvéniles ou larvaires n'a été observé dans l'alimentation des adultes lors de cette étude.

Se analizó el contenido estomacal de listados capturados con caña en 1981–1982 frente a la costa Sur de Brasil, con el fin de constatar la presencia de larvas y juveniles de listado. Se evaluó el porcentaje de presencia, porcentaje del número y porcentaje del volumen. De los 1041 estómagos examinados, 436 estaban vacíos. El volumen medio del alimento encontrado en todos los estómagos analizados era de 36,9 ml, de los cuales 18,9 ml eran de cebo y 18,0 ml presas. No se encontraron larvas ni juveniles de listado en los estómagos de los adultos analizados.

1. Introduction

A Brazilian skipjack pole-and-line fishery has been developing in the Rio de Janeiro area since 1979 (Figure 1). Skipjack is one major tuna species harvested at under maximum sustainable yield in the tropical and subtropical oceans (Kearney 1978; Evans et al. 1981), and therefore, estimation of the fishery potential requires information on the distribution and concentration of its spawning stock. One technique used to determine the existence of a spawning stock is to quantify the distribution of its larvae. Obviously, the presence of large numbers of larvae would indicate a spawning stock occupies an area.

Knowledge of the distribution and abundance of juvenile skipjack is limited. Occasionally, specimens have been found in experimental plankton hauls or in the stomachs of apex predators (Kearney 1978). From ichthyoplankton surveys Matsuura (1982a) and Nishikawa et al. (1978) report larvae in warm tropical waters north of the study area (Figure 1).

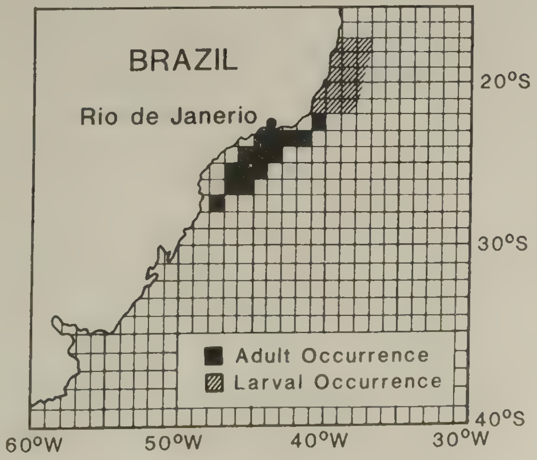

Figure 1. Shaded area indicates occurrence of larval and adult skipjack tuna (Matsuura 1982a).

Juvenile skipjack have been found in the stomachs of adult skipjack captured off west Africa and in the Caribbean (Dragovich 1970a; Dragovich and Potthoff 1972; Suarez-Caabro and Duarte-Bello 1961; Klawe 1961). Their occurrence in the diet of central and south Pacific skipjack caught by pole-and-line has been used to deduce their distribution and abundance (Waldron and King 1963; Nakamura 1965; and Argue et al. 1983).

The primary objective of this study was to quantify the occurrence of larval and juvenile skipjack in the stomach contents of adults from the Brazilian fishery. This information could then be used to derive conclusions on their distribution and abundance in this area.

2. Materials and Methods

Stomach samples for this study were collected on a monthly basis from October 1981 to December 1982 from skipjack caught off Rio de Janeiro (Figure 1). U.S. National Marine Fisheries Service (NMFS) personnel collected stomachs from frozen fish transhipped to Puerto Rico, and Superintendencia do Desenvolviemento da Pesca (SUPEDE) personnel sampled fish landed locally in Rio de Janeiro. Fish from the Puerto Rican source were sampled within one month of being caught; fish from the Brazilian source were sampled three to five days after the recorded catch date. The sampling design required collecting approximately fifteen stomachs from each 10 cm length group, measured to the nearest cm per month. However, the number of stomachs collected was dependent on the catch size distribution. Once the stomach was removed from the fish, it was preserved in 10% buffered formalin and shipped to the Southwest Fisheries Center (SWFC) for analysis.

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Stomachs were examined from 1041 fish between 44 and 81 cm fork length. In the laboratory each stomach was opened. The volume of the food bolus was measured, and the contents were identified to the lowest possible taxon. The taxonomic groupings were then measured by volumetric displacement, and the individuals counted. Whole undigested fish were identified by comparing external characters with those described in published keys or with identified museum specimens from Scripps Institution of Oceanography, La Jolla, California. Digested animals, particularly juvenile scombrids, were identified by vertebral, gill raker, and fin ray counts, as well as other skeletal characteristics, described by Potthoff and Richards (1970), Miller and Jorgenson (1973), and other published keys. The bait consisted of the Brazilian sardine (*Sardinella brasiliensis*), the scaled sardine (*Harengula jaguana*), and the Argentine anchovy (*Engraulis anchoita*); however, other fish families may have been included in the captured bait.

An index of relative importance was calculated for each prey type in terms of numbers, volumes, and frequencies (Pinkas et al. 1971):

$$IRI = (N + V)F$$

where:

N = numerical percentage
V = volumetric percentage
F = frequency of occurrence percentage

These data were stratified by fish length (seven 5-cm categories) and month.

3. Results and Discussion

Of the 1041 stomachs that were examined, 436 were empty. The mean volume of food in all stomachs examined was 36.9 ml, of which 18.9 ml was bait and 18.0 ml was prey. No larval or juvenile skipjack were found in the stomach contents. The results of the other prey data are to be published at a later date.

The multiplicity of prey found in this as well as other studies indicates that tunas are perhaps non-selective feeders, and stomach contents are probably determined by prey availability (Alverson 1963; Hotta and Ogawa 1955; Batts 1972b; Perrin et al. 1973; Argue et al. 1983). Therefore, if the larval and juvenile skipjack were available in significant numbers, then one would expect them to occur in the diet of the adults.

Goldberg and Au (this volume) found no evidence of spawning in skipjack collected from the Brazilian fishery. These results are consistent with the absence of larval and juvenile skipjack in the diet of the adults in this study.

The southernmost distribution boundary for larval skipjack is the 24°C surface isotherm (Argue et al. 1983). Matsuura (1982a) found no larval skipjack in ichthyoplankton surveys south of 21°S latitude in this area, where temperatures range from 21°C to 24°C (Evans et al. 1981).

These results are consonant with those of Argue et al. (1983); juvenile skipjack were absent from samples of adult stomachs taken in subtropical south Pacific waters. The adult skipjack in this investigation did not feed on their young. The absence of cannibalism suggests that larvae and juveniles were not sufficiently abundant to serve as forage of the adults, and therefore, probably do not occur in this cooler southern water (see also Matsuura this volume).

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Evaluation of Methods used by the South Pacific Commission for Identification of Skipjack Population Structure

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The use of data from blood genetics, tagging, growth, maturity, juvenile occurrence, and parasite studies for examining skipjack population structure is discussed in light of experience by the Skipjack Survey and Assessment Programme of the South Pacific Commission. Results from analyses of these data support several different hypotheses of skipjack population structure in the Pacific Ocean. This confusion reflects, in part, the limited information content of these data for inferring population structure. Therefore unconditional support for any one hypothesis is misleading, particularly as the potential for fishery interactions differs markedly amongst the hypotheses.

Before choosing a most likely hypothesis of skipjack population structure, gaps in the basic biological data, specifically geographical distribution of spawning and movement of pre-recruits, should be filled. Obtaining comprehensive new data will be costly and time-consuming and will not overcome inherent weaknesses of the traditional methods. There is a need to weigh the benefits to be gained from improved knowledge of population structure against the benefits to be gained from a better understanding of interaction amongst components of the rapidly expanding fishery for skipjack.

L'utilisation de données provenant d'études sur le sang, la génétique, le marquage, la croissance, la maturité, la présence de juvéniles et les parasites est traitée à la lumière de l'expérience acquise dans le cadre du Programme de Recherche et d'Evaluation du Listao de la Commission du Pacifique sud. Les résultats obtenus par l'analyse de ces données viennent appuyer diverses hypothèses concernant la structure de la population de listao dans l'océan Pacifique. Cette confusion reflète en partie l'intérêt limité de ces données en ce qui concerne une information permettant de formuler des hypothèses quant à la structure de la population. Une adhésion sans réserves à l'une quelconque des hypothèses peut donc induire en erreur, surtout du fait que le potentiel d'interaction des pêcheries diffère de façon sensible selon les hypothèses.

Avant de procéder au choix de la structure la plus probable de la population de listao, il convient de combler des lacunes dans l'information de base sur la biologie, en particulier pour ce qui est de la distribution géographique de la ponte et des déplacements des pré-recrues. L'obtention d'une information exhaustive est coûteuse, demande beaucoup de temps, et n'éliminera pas les faiblesses inhérentes aux méthodes traditionnelles. Il est nécessaire de jauger les avantages qui découleront de connaissances plus amples sur la population, par rapport à ceux que représenterait une meilleure compréhension des phénomènes d'interaction entre les divers éléments de la pêcherie de listao, laquelle se développe rapidement.

Se debate el empleo de datos de genética de la sangre, marcado, crecimiento, madurez, aparición de juveniles y estudios de parásitos para examinar la estructura de la población de listado, a la luz de la experiencia del Programa de Evaluación y Encuesta sobre el Listado, de la Comisión del Pacífico Sur. Los resultados de los análisis de estos datos apoyan varias y diferentes hipótesis sobre la estructura de la población del listado en el Pacífico. Esta confusión refleja, en parte, la escasez de la información contenida en estos datos, lo que no permite sacar una conclusión sobre la estructura de la población. Por lo tanto, un apoyo incondicional de cualquiera de estas hipótesis conduciría al error, especialmente debido a que el potencial de interacciones en la pesquería difiere mucho entre dichas hipótesis.

Antes de escoger la hipótesis más plausible sobre estructura de la población del listado, se deben rellenar los vacíos existentes en los datos biológicos básicos, y específicamente en lo que se refiere a la distribución geográfica del desove y movimiento de los pre-reclutas. El obtener datos nuevos y suficientemente amplios será costoso y largo y no compensará la inherente deficiencia de los métodos tradicionales. Es necesario comparar los beneficios que se podrían obtener de un mejor conocimiento de la estructura de la población con los beneficios que resultarían de un mejor entendimiento de la interacción entre los componentes de la pesquería de listado, en rápida expansión.

1. Introduction

Before the South Pacific Commission's Skipjack Survey and Assessment Programme (Kearney 1983) commenced, Fujino (1970b, 1972, 1976) had concluded from an analysis of blood electrophoretic data that there were two genetically isolated subpopulations of skipjack, one in the central/eastern Pacific and one in the western Pacific. Later, Sharp (1978) proposed five skipjack subpopulations in the Pacific Ocean using similar data. The degree to which fisheries exploit skipjack of the same genetic origin could differ greatly depending on which, if either, of these hypotheses was true. Skipjack differing in genetic origin might also be expected to differ in productivity. If so, fishing strategies designed to optimize yield might need to be varied amongst fisheries; clearly a first step is to describe skipjack population structure.

Assessments of skipjack population structure by the Skipjack Programme, based on electrophoretic analysis of skipjack blood samples and analysis of tag and recovery data, were published soon after fieldwork finished (SPC 1980, 1981d). Since then, further analysis of skipjack migrations (SPC 1981a), growth (Sibert et al. 1983), distribution of spawners and juveniles (Argue et al. 1983), and occurrence of parasites (Lester 1981; Lester et al. MS) has provided a wider data base from which to evaluate methods for identifying of skipjack population structure.

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2. Definitions

There is often ambiguity and confusion associated with use of the terms "stock" and "subpopulation". In a fishery context, a stock is a subdivision of a population that is vulnerable to a fishery. In a biological context, the term subpopulation is usually substituted for stock, with subpopulation implying a subdivision based on a degree of genetic isolation (SPC 1976). These terms are not compatible, because only in special circumstances would they describe the same subdivisions of a population.

By defining a stock as those fish vulnerable to a fishery, their spatial distribution could be considered simply as the area of the fishery where individuals from one or more subpopulations might be present. A subpopulation would normally cover a larger area due to movement of individuals beyond the operating range of the fishery. In the case of several subpopulations, it is likely that their spawners would be separated geographically, or temporally, and would not be exploited by the same fishery.

Both stocks and subpopulations may be considered in terms of short or long time periods. For example, a stock could be simply the fish vulnerable to one unit of gear on a time scale of part of one day. At the other extreme, on a time scale of many generations, a stock could include all fish that were vulnerable to the fishery and whose descendants become vulnerable to the fishery. So defined, a stock could encompass vulnerable adults from one or more subpopulations. For a subpopulation, the time scale could span many thousands of generations and involve a degree of genetic isolation bordering on that required for speciation. Alternatively, a subpopulation might simply refer to a breeding group, that is a portion of the population that tends to breed predominantly amongst its own members, and whose integrity might change with, for example, annual fluctuations in the environment.

The choice of an appropriate definition depends on the objectives of the investigation. For most fishery investigations, pragmatism dictates this choice, and investigators attempt to identify the biological unit(s) which are responsible for the bulk of production that a fishery harvests, and which are reproductively isolated to the extent that their production is self-sustaining. Such units, which have at least some properties of a subpopulation, are commonly called stocks.

3. Genetic Analysis of Skipjack Blood Samples in Conjunction with Tagging Data

The Skipjack Programme used combined data from blood sampling and tagging to test hypotheses relating to skipjack movement and population structure. The Programme obtained fifty-eight blood samples consisting of 100 individual skipjack from each of fifty-eight schools, and tagged a total of 32,427 skipjack from these schools. None of the female skipjack from which blood specimens were taken were running ripe; only a few had ripe gonads. Forty two loci were analysed for electrophoretically detectable polymorphisms (Richardson 1983). Three loci showed polymorphisms that were suitable for a traditional population analysis: of these, only serum napthyl esterase exhibited sufficient geographic variability to be suitable for detailed consideration.

The Skipjack Programme hosted two workshops at which specialists in the fields of population genetics and fishery population biology met with the Programme's scientists to jointly consider the statistical analyses and resulting interpretations of the combination of blood genetics and tagging data. Both workshops dealt with additional published and unpublished blood genetics data for the eastern, central and western Pacific Ocean that were provided by participants. The results and interpretations from these workshops (SPC 1980, 1981d) were summarized in (SPC 1981b), and are expanded here as follows.

3.1 RESULTS AND INTERPRETATIONS

Esterase gene frequencies in skipjack showed a pronounced longitudinal gradient across the study area, with flattening of this gradient occurring to the east of 120°W longitude (Figure 1). This gradient is consistent with the concept of a cline. Underlying the clinal hypothesis is the assumption that ". . . the probability of two fish mating is a decreasing function of the distance between their birth places . . ." (SPC 1981d). In other words, there is an isolation-by-distance component to the population structure. Acceptance of this model implies that there are no genetically isolated skipjack subpopulations in the study area, which is contrary to hypotheses advanced by both Fujino and Sharp using different sets of blood genetics data. This conclusion is supported by Graves and Dizon (this volume) who found no evidence of genetic isolation between skipjack from the Atlantic and Pacific oceans, using the powerful technique of restriction enzyme analysis of mitochondrial DNA.

Existence of the esterase gradient was considered to be strong evidence that the Pacific skipjack do not comprise a single panmictic population, in which all adults of one generation have an equal chance of mating.

The gradient in esterase gene frequency is consistent with two possible distributions of skipjack spawning, one being a relatively even distribution of spawning in tropical waters across the study area. One could also view the gradient as the zone of contact between skipjack from two or more centres of high spawner density (breeding groups) perhaps at the approximate extremes of the study area or beyond. Thus the gradient could represent a mingling primarily of migrants from the centres of spawning, or a zone of weak hybridization where there may be lowered breeding success. The similarity between eastern Pacific esterase gene frequencies (east of 120°W in Figure 1) and those from French Polynesia (155°W) suggests that most skipjack from the eastern Pacific, where reproduction is thought to be much less successful (Klawe 1963), could have the same genetic origin as those in French Polynesia. Observations on the occurrence of skipjack juveniles in stomachs of adults and on gonad development (Section 6.) support the view that there are several centres of skipjack spawning. An isolation-by-distance model of skipjack reproduction is consistent with either an even distribution of spawning or several geographical centres of spawning.

The tagging data implied that there is some mixing of adult skipjack over a wide area (Section 4.). If such mixing involved reproducing skipjack and hence genetic exchange, it would have to be offset by some degree of selection in order to maintain a cline.

No obvious relationship was evident between esterase gene frequency for particular skipjack schools and subsequent movement of tagged skipjack from these schools, nor was there a significant relationship between net movement of tagged skipjack from each school and the difference between actual gene frequency and gene frequency estimated from the regression line in Figure 1 (SPC 1981d). It was concluded that gene frequency for a school was not a predictor of skipjack movement.

The workshop participants concluded that a clinal population structure was a reasonable alternative hypothesis to the isolated subpopulation hypotheses advanced by Sharp and Fujino.

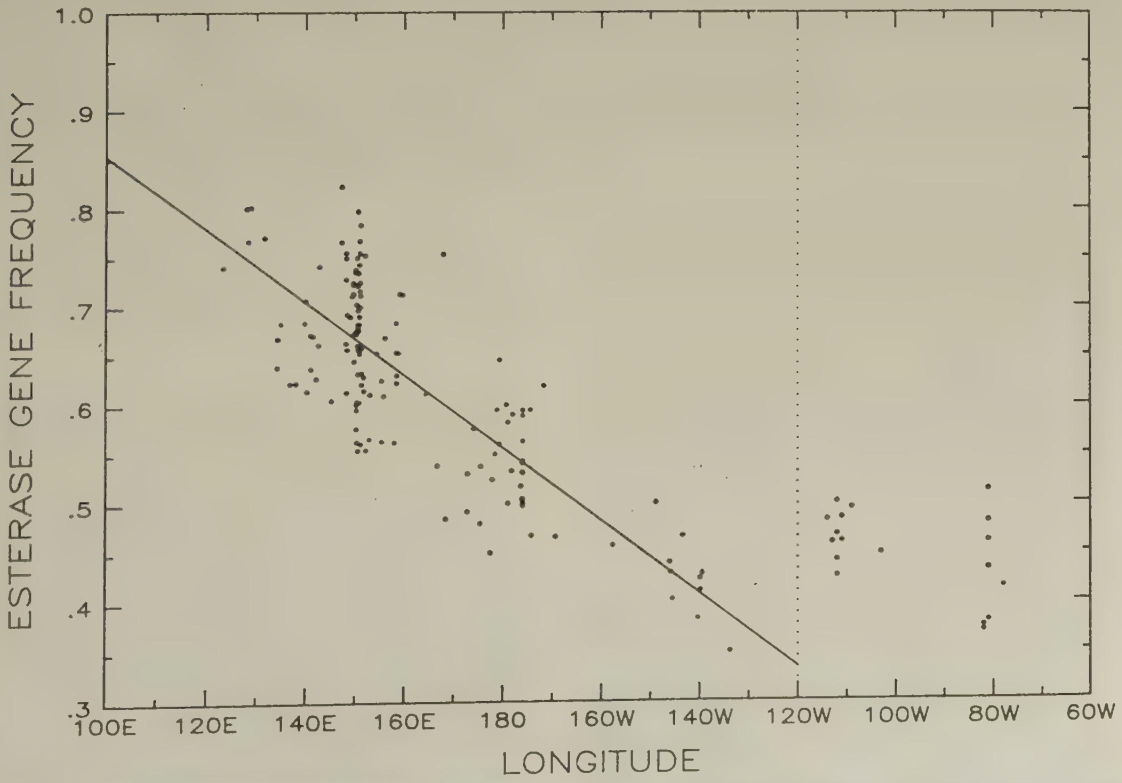

Figure 1. Skipjack serum esterase gene frequency versus longitude of the sample location. The regression line was fitted to the data for 145 samples to the left of 120°W (dotted line); the correlation coefficient was −0.81 ($p<0.01$). Eighteen samples from eastern Pacific waters are to the right of the dotted line. Figure redrawn from (SPC 1981d).

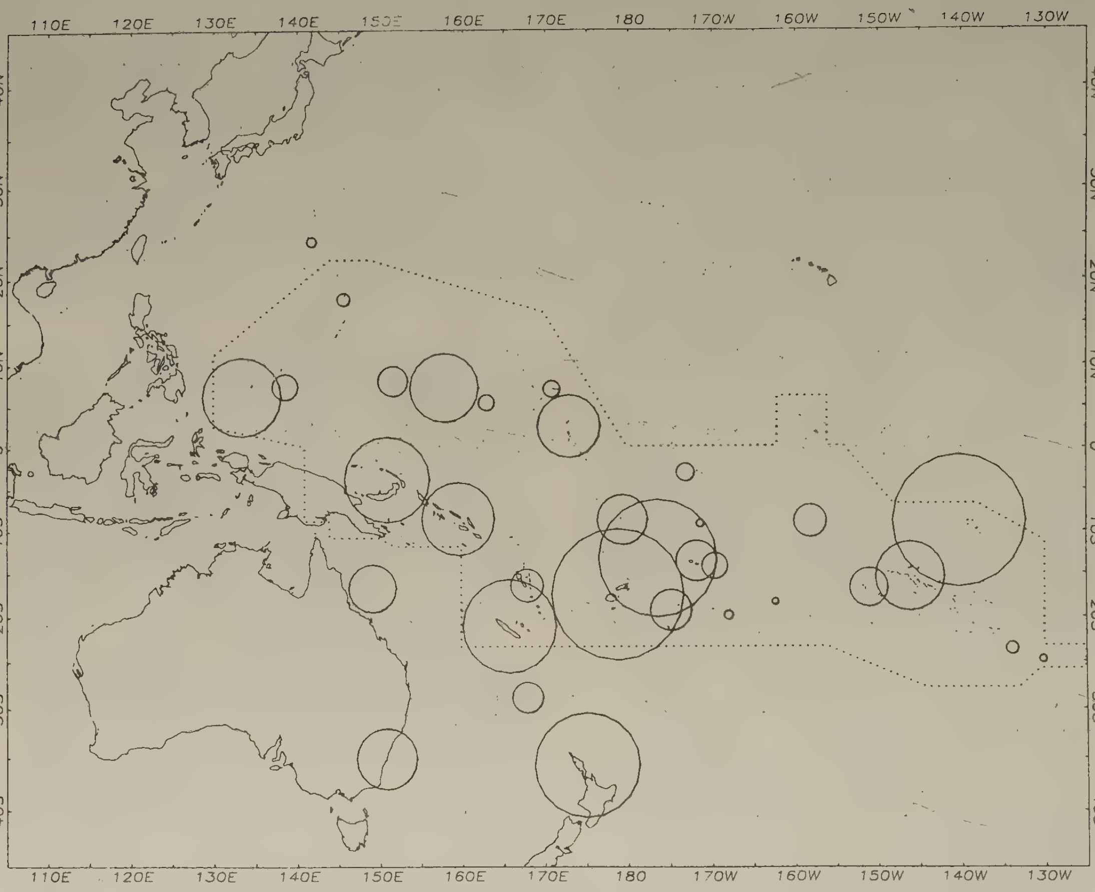

Figure 2. Distribution of tag releases (circles) and boundaries of the South Pacific Commission Region (dotted line). The circles are centred on each country, territory or subdivision thereof, and are proportional to the number of tagged skipjack released in each location. Figure from Kleiber et al (1983b).

4. Tagging

Between October 1977 and August 1980, 140,433 skipjack were tagged and released. The itinerary of the tagging vessel was planned so that releases of tags in the area of the South Pacific Commission and adjacent areas where skipjack were known to be abundant would be as widespread as possible (Figure 2). Migration patterns that became evident from recoveries of these releases were expected to clarify skipjack population structure.

4.1 MIGRATION

Figure 3 presents a selection of tag returns plotted as straight line arrows between tagging and recovery location. The impression from Figure 3 is one of considerable mixing of skipjack. It should be noted, however, that the overall impression of many wide-ranging migrations in Figure 3 does not reflect the average case for all tag recoveries. This figure overemphasizes long distance, relatively rare migrations, due to the procedure used to select recoveries for the figure (see caption Figure 3). The lack of apparent movement beyond the area surveyed may reflect poor chances of recovery as a result of low fishing effort, and environmental barriers to migration at high latitudes (skipjack are seldom encountered polewards of 40° latitude or in waters cooler than 16°C).

Figure 4 shows that tag recoveries in a particular area (Solomon Islands) decrease as the distance between the recovery area and tag release site increases. For the total study area, the majority (86%) of tag recoveries were made less than 250 nautical miles from their release site and within 180 days of tagging (Figure 5). It was only within the smaller group of skipjack that were at large for more than 180 days (bottom graph in Figure 5) that long-distance migrations were common. This suggests that few skipjack of the size that were tagged were available to fisheries for long enough to be recovered at great distances from their release site.

There are several limitations to the use of tag migration data for examination of skipjack population structure. Curved pathways, if present, are not readily

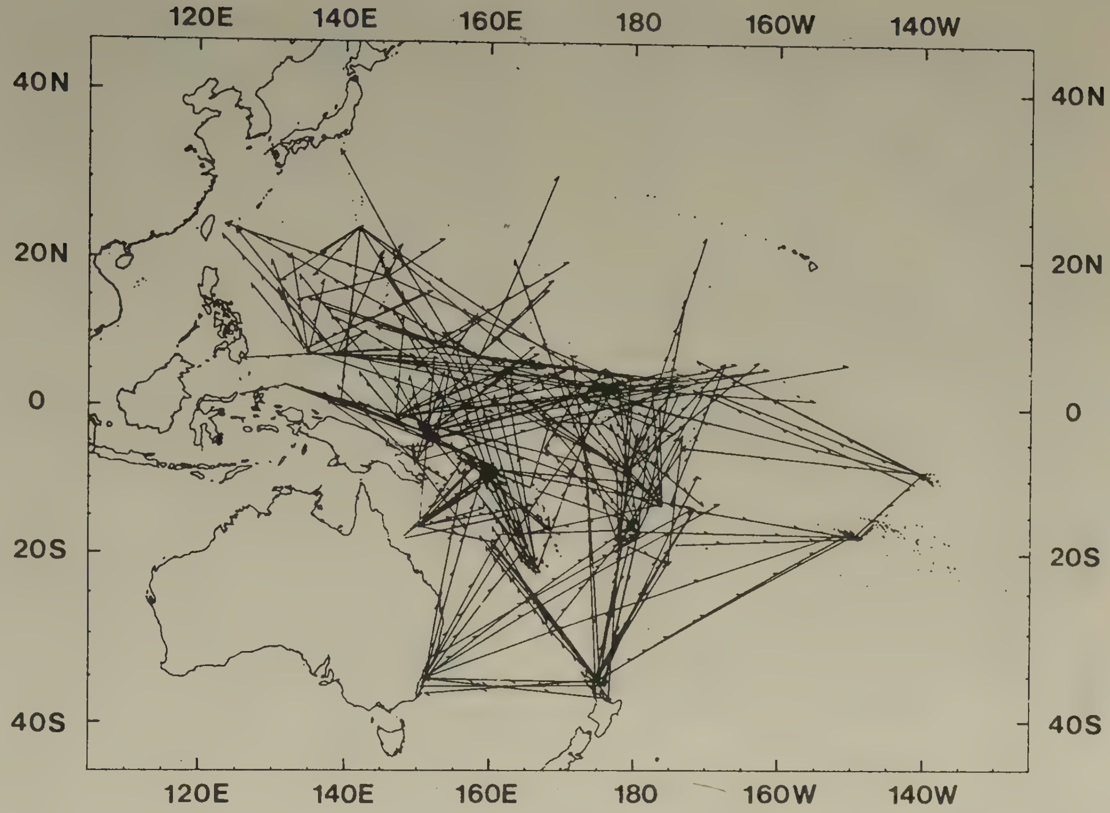

Figure 3. Straight line representations of movements of skipjack tagged by the Skipjack Programme and subsequently recovered. Movements plotted have been selected to show no more than two examples between any pair of ten degree squares, one in each direction, and no more than one example of movement wholly within any ten degree square. Tick marks on the arrows represent 90-day periods between release and recapture. Figure redrawn from (SPC 1981a).

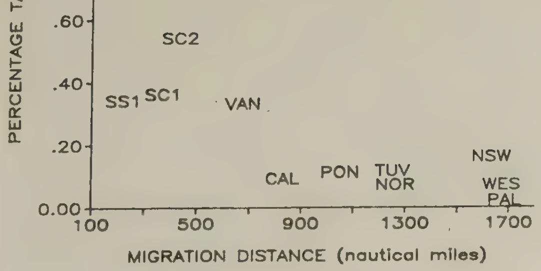

Figure 4. Relationship between tag recovery rate by Solomon Islands pole-and-line vessels and average distance travelled by tagged skipjack released in countries (areas) external to the Solomon Islands fishing area. Abbreviations are explained in the Appendix. Figure redrawn from Argue and Kearney (1982).

discerned from straight line arrows between tagging and recovery location. Additional confusion can result if the pathways themselves are shifting either seasonally or on other time scales. This situation is further complicated because tags were not released simultaneously over the whole of the study area. Care must be taken not to give undue weight to long migrations, which are the ones that stand out in Figure 3, but are hardly the most common (Figure 5). Random movement adds to the difficulty of identifying underlying directed movements, if such exist. Another difficulty results from the non-uniformity of fishing intensity in time and space. For example, many tagged skipjack were released within commercial fisheries, hence, to some degree, the distributions of tag recoveries in Figure 5 reflect the nearby location of fishing effort. Without taking this factor into account, any conclusions about migration patterns and distances moved could be partly or totally an artifact of the distribution of fishing effort. There is little hope of solving this problem without catch and effort statistics for all fisheries responsible for recapturing and returning tags. Unfortunately, adequate fishery statistics are not yet available to the South

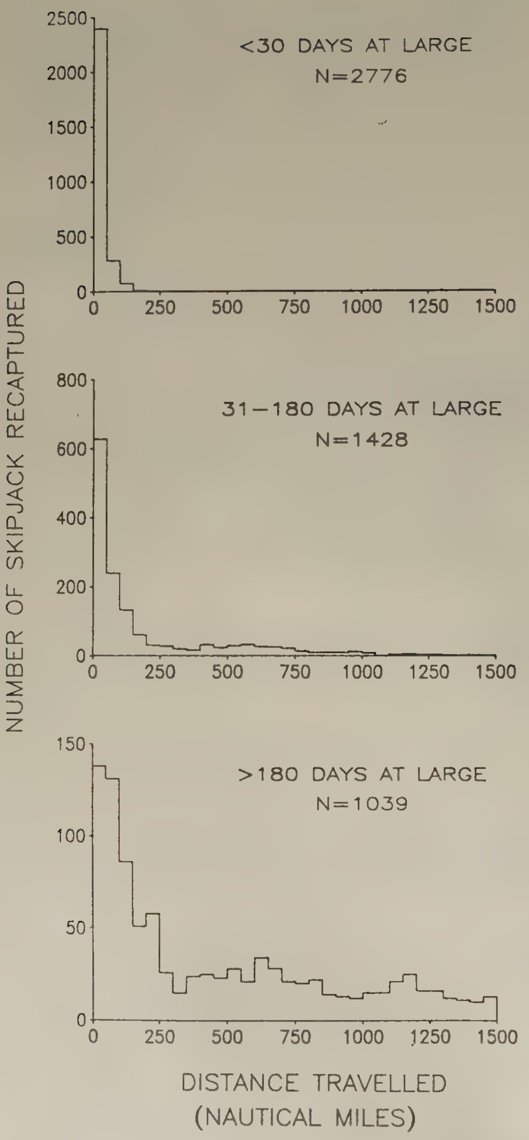

Figure 5. Numbers of skipjack tag recoveries by distance travelled and time-at-large. Data are for tag returns received by 4 November 1982. Recaptures for 96 fish, which travelled more than 1500 miles, are included in the sample sizes of the middle and lower graphs, but are not shown.

Pacific Commission for the whole of the period of tag releases and recoveries. Finally, without knowing the reproductive stage of each skipjack at the time it was tagged and at the time it was recovered, it is impossible to say whether movements of tagged fish represent adults homing to spawning areas, or simply the movement of dispersing fish to any number of spawning or feeding areas.

4.2 Level of Immigration

Results in Section 4.1 did not take fishing intensity into account. Kleiber et al. (1983a) describe an immigration statistic that does this and expresses immigration as the percentage of recruitment in a "destination" country that arose from immigrants from a "donor" country. Table 1 presents these percentages for countries in the study area for which tags were recovered and catch statistics were available. Although levels of immigration were generally low (<15%) between fisheries in these countries, they were not insignificant and confirm that there is mixing of adult skipjack and potential for significant genetic exchange over large distances.

Table 1. Interaction between stocks fished by donor and destination countries expressed as the percentage of recruitment in the destination country estimated to arise from immigrants from the donor country. Table from Kleiber et al. (1983a) and SPC (1984).

Donor Country	Destination Country	Interaction	Approximate Nautical Miles Between Countries
Solomon Islands	Papua New Guinea	1–5%	550
Papua New Guinea	Solomon Islands	8–12%	550
New Zealand	Fiji	14%	1200
New Zealand	French Polynesia (Society Islands)	9%	2340
Fiji	New Zealand	<1%	1200
Federated States of Micronesia	Solomon Islands	1%	1100
Federated States of Micronesia	Papua New Guinea	1%	1100
Papua New Guinea	Marshall Islands	<1%	1400
Northern Mariana Islands	Federated States of Micronesia	17%	700
Palau	Marshall Islands	2%	2300
Federated States of Micronesia	Marshall Islands	37%	1200
Federated States of Micronesia	Northern Mariana Islands	11%	700

5. Growth

Geographical variation in skipjack growth might also suggest biological subpopulations. Analysis of covariance was used to compare growth increments (length at recovery minus length at tagging) among countries and time periods. A Taylor series was used to express growth increments as a sum of derivatives of the von Bertalanffy growth model, thus accounting for different size at tagging and days at liberty. Results demonstrated that skipjack growth increments varied significantly among countries and time periods (Sibert et al. 1983). In Figure 6 these results are illustrated by point estimates and joint confidence intervals for L_∞ and K of the von Bertalanffy model, for some of the country data sets used in the analysis of covariance, as well as for eastern and western Pacific data sets that were matched to have times at liberty and sizes at release as similar as possible. Overlapping confidence intervals are a feature of these results. For the few cases in which confidence intervals do not overlap, it is hard to discern a geographical pattern that could be interpreted as due to different subpopulations. Sibert et al. (1983) ascribed these differences in growth parameters to differences in environmental conditions (e.g. temperature, salinity, food supply) conducive to growth.

6. Distribution of Spawners and Juveniles

Measures of timing and geographical distribution of spawning are important for understanding population structure. Gonad indices (see caption Figure 8) were calculated for female skipjack by month and by 12° latitude, 10° longitude cells (Argue et al. 1983). High index values (>50) are associated with skipjack whose gonads have a high percentage of eggs that are ready to be spawned (Raju 1964a). Similar temporal and spatial analyses of the numbers of juvenile skipjack per 100 adult skipjack predators were carried out. This is an index of apparent abundance of juveniles, previously used by Yoshida (1971) and Mori (1972b) to examine seasonal and geographical variation in relative abundance of juvenile skipjack.

Argue et al. (1983) discuss the results of these analyses in detail. They suggest that during the survey period of the Skipjack Programme, skipjack spawning in tropical waters was most intense, south of the Equator, during the warmer months, October to March, and that skipjack juveniles and spawning adults were concentrated within the study area in two locations — one amongst the Marquesas and Tuamotu Islands, and the other in the waters of Papua New Guinea, Solomon Islands and Vanuatu (Figure 7). In these regions apparent abundance of skipjack juveniles increased with increasing maturity of female skipjack gonads (Figure 8). These results imply a similar distribution of spawning and juvenile skipjack in the study area. At first glance these results support the idea that there are separate subpopulations. However, as mentioned in Section 3., existence of areas of higher spawning intensity does not conflict with the concept of a cline. As well, there was evidence of some spawning throughout the year in all tropical waters surveyed by the Programme, which is consistent with the hypotheses of a clinal population structure and an even distribution of spawning. Finally, large-scale oceanographic events may alter the distribution of juveniles and spawning adults, and there are geographic gaps in the available data. These factors suggest caution when using the above results to support models of population structure.

7. Parasites

Internal and external parasites carried by skipjack in different parts of the Pacific may be used to clarify patterns of movement and population structure of skipjack. In December 1979, the Programme began collecting viscera and gills from five skipjack per school, for a maximum of three schools per day, for subsequent parasite analysis. Counts were made of the numbers of larval *Tentacularia coryphaenae* (a tapeworm common in skipjack) that were visible in the walls of the body cavity of skipjack sampled from each school.

Skipjack samples for parasite analysis were taken over a wide range of tropical waters, and also from subtropical waters of New Zealand and Norfolk Island. Preliminary results from a multivariate analysis presented by Lester (1981) showed that the

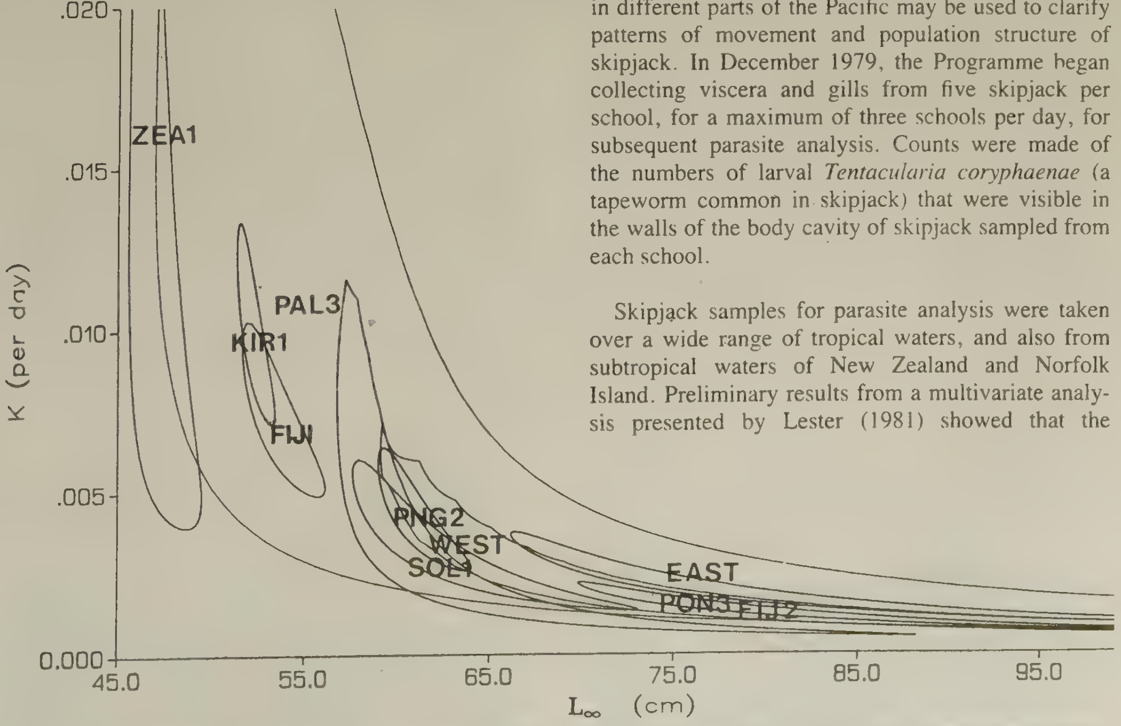

Figure 6. Approximately 95 percent joint confidence regions for K and L∞ for data sets based on Skipjack Programme tag releases and recoveries. Position of the abbreviations indicate point estimates of parameters for corresponding geographic regions and times. Abbreviations are explained in the Appendix. Figure from Sibert et al. (1983).

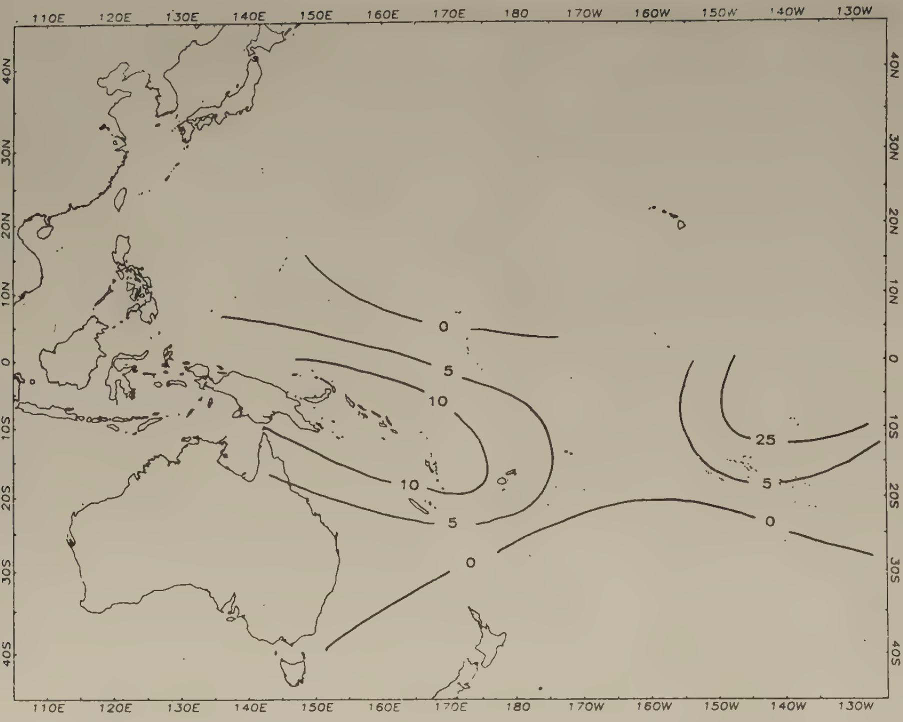

Figure 7. Isopleths of apparent abundance of juvenile skipjack (numbers of juveniles per 100 skipjack predator stomachs). Samples were collected between October 1977 and August 1980 and isopleths were estimated from average values for samples taken within 12° latitude by 10° longitude cells during October to March and April to August time periods. Figure redrawn from Argue et al. (1983).

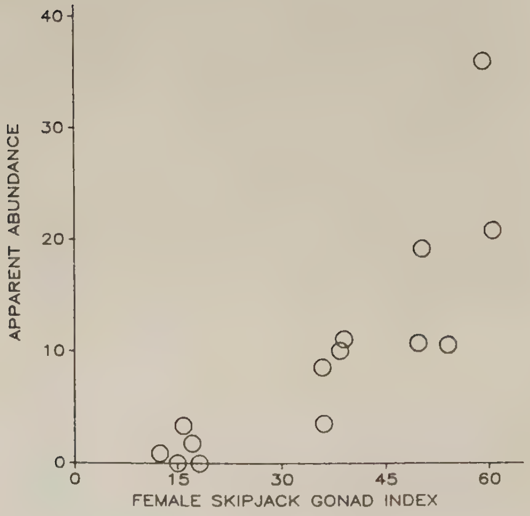

Figure 8. Relationship between skipjack juvenile apparent abundance and female skipjack gonad index, for samples of adult skipjack from 12° latitude by 10° longitude cells in the centres of high skipjack juvenile apparent abundance in Figure 7. The correlation coefficient was 0.84 ($p<0.01$). Gonad Index = 10^7 (gonad weight gm/(fork length mm)^3). Figure redrawn from Argue et al. (1983)

skipjack caught in widely separated tropical areas carried similar long-lived parasites, but that skipjack caught in New Zealand had different parasites from those caught in tropical waters to the north. New Zealand fish did carry tropical parasites at approximately the same level as skipjack caught in the tropics, which suggested that New Zealand fish were recent arrivals from the tropics (Lester et al. MS). These results provided no evidence of discrete skipjack subpopulations.

8. Evaluation

8.1 What Life History Stage was Sampled?

To infer population structure from biological or tagging data, it is important to know the life history stage of the sampled or tagged skipjack. Frequently, this information has been absent. For many samples taken for blood analyses, there were no measures of maturity, hence these samples could consist of mature pre-spawning skipjack, of post-spawning skipjack, of immature skipjack, or of some combination. Similarly, the tag releases could have been of non-migrant skipjack, of skipjack that had concentrated in spawning areas, of skipjack traveling along possible dispersal or migration pathways, or of skipjack homing to spawning area.

Not knowing which life history stage was sampled or tagged limits the inferences one can make regarding genetic exchange between areas. Inability to estimate genetic exchange confuses the choice of an appropriate population model.

8.2 Dispersal, Migration, Selection

In the case of the blood genetics data, the observed esterase gradient (cline) could be maintained by various combinations of movement and selection[1]. If the esterase cline was maintained by high selection on each generation of very young skipjack, then dispersal of older fish could be extensive and the cline would still be maintained. To maintain the cline when selection is negligible requires that adults disperse little, although they could migrate extensively as long as they returned home to spawning areas.

Various combinations of movement and selection have different potentials for fishery interactions. Table 2 presents examples of these combinations and their potential fishery interactions. At this time, neither the electrophoretic data nor the analysis of tagging data allow one to choose with confidence from the different alternatives of how the cline may be maintained.

Table 2. The potential for fishery interactions under different levels of selection, dispersal and migration/homing. Table adapted from SPC (1981b).

Selection	Dispersal	Migration/ Homing	Potential for Fishery Interactions
Clinal Hypothesis — Even Distribution of Spawning			
High	Extensive	Negligible	High
High	Negligible	Negligible	Low
Negligible	Negligible	Extensive	High
Negligible	Negligible	Negligible	Low
High	Negligible	Extensive	High
Clinal Hypothesis — Two or More Breeding Units			
High	Extensive (but little between units)	Negligible	High in mixing zone Low between breed-ing areas
Negligible	Negligible	Extensive	High in mixing zone and between breeding areas

8.3 Environmental Variability

Surface waters in the tropical Pacific are thought to undergo major physical changes, such as the strong El Niño warming that peaked in 1983 in the eastern and central Pacific (Rasmusson et al. 1983). These, in turn, may greatly alter the geographical distribution of productivity throughout the pelagic food chain. It follows, then, that mobile pelagic species such as skipjack may respond by altering spawning distribution and intensity, recruitment of juveniles, growth, and movement patterns. If so, measures of these variables over relatively short time periods would be of limited value for inferring population structure.

8.4 Pre-Recruits

A major shortcoming to date of blood genetics sampling, parasite sampling and tagging is that these techniques have focused entirely on post-recruitment skipjack. Larval and juvenile skipjack (less than 15 cm in length) could undergo extensive movement simply by passive association with ocean currents. Young skipjack of up to 45 cm may undergo feeding movements of great distance from areas in which they were spawned. For example, Kearney (1978) hypothesized that juvenile and young skipjack followed the 20°C isotherm in a poleward direction until they reached areas where surface waters approached 20°C. This hypothesis is supported by data in Argue et al. (1983). Such movement, if substantiated, would imply a potential for long and short term genetic exchange, and fishery interactions, over large distances.

9. Discussion and Conclusions

It is as important to understand the limitations of data collected by following a particular line of research, as it is to recognize alternative hypotheses arising from the data. To this extent we feel that results (summarized in Table 3) from our analysis of a suite of data (blood genetics, tagging, growth, maturity, juvenile occurrence, parasite infestations) pertaining to skipjack population structure has been most fruitful. The clinal population hypothesis was put forward (SPC 1980, 1981d) as an alternative to the isolated subpopulation hypotheses (Fujino 1970b, 1976; Sharp 1978). Distribution of juveniles and spawning offered conditional support to the isolated subpopulation hypotheses, although possible modification of these distributions through environmental change should be noted. Tagging, growth, and parasite data, as discussed, have weaknesses when used to investigate population structure, but on balance, they offered conditional support for the clinal hypothesis. In brief, none of the analyses considered by the Skipjack Programme provided sufficiently clear cut results to support a particular population structure hypothesis. Consequently, we conclude that unconditional support for any of the hypotheses, such as that proposed by Fujino et al. (1981) for the two isolated subpopulations hypotheses, is misleading and predictions of skipjack movement based on either hypothesis (Fujino 1972; Richardson 1983) are at best premature.

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[1] As used here, dispersal refers to movement of skipjack to different breeding locations at varying distances from where they were spawned; migration refers to movement (perhaps for feeding) of skipjack to areas at varying distances from where they were spawned, followed by homing to the area where they were spawned

Table 3. Summary of results from methods used by the South Pacific Commission (SPC) to investigate skipjack population structure

Method	Results Pertaining to Population Structure	Management Utility
Blood genetics samples	SPC analyses support a clinal hypothesis, but it is unclear how the cline is maintained. Other investigators using different blood genetics data have inferred genetically isolated subpopulations.	Subjective and conflicting evidence of potential for fishery interactions.
Tagging	No oceanic barriers to migration. Conditional support for clinal hypothesis.	Quantification of population parameters and fishery interactions.
Growth	Estimates of growth parameters vary in space and time suggesting a strong environmental rather than genetic effect.	Estimation of yield.
Juvenile distribution/ maturity	Juvenile and spawning skipjack appear concentrated at longitudinal extremes of the study area. Conditional support for isolated subpopulation hypotheses.	Delineation of areas where spawning may be concentrated.
Parasites	No evidence of discrete subpopulations.	Evidence of movement between tropical and subtropical waters.

Our analyses have pointed out some shortcomings of traditional approaches to investigations of population structure. These include gaps in knowledge of the relative abundance, distribution and movement of skipjack at all life history stages, but particularly for spawners and for young skipjack prior to recruitment. These gaps weaken inferences of population structure made from the traditional data, particularly data arising from opportunistic sampling of adults. In the past, many questionable assumptions were necessary to get around these limitations. This reduced the scientific and management value of results from investigations on population structure of skipjack.

Obtaining sufficient new data to distinguish between hypotheses, using traditional methods in an area as large as the western and central Pacific, will be costly and time consuming. Before embarking on this work it is important to consider to what extent its successful completion would help to achieve overall research objectives. In the Pacific Ocean there is yet no evidence that skipjack recruitment is being impaired by levels of catch. Nevertheless, dramatic changes have taken place in the fishery. Catch has apparently increased substantially in a small portion of the central and western Pacific (Kearney 1983), but little reliable statistical information is available. With increased catch the potential for within-generation interactions between fisheries and fishing gears has grown. Lack of statistics and the potential for fishery interactions are of great concern to countries deriving revenue from the skipjack resource. Thus there is a need to weigh benefits that improved knowledge of population structure would bring against those to be obtained from improved information on fishery interactions and fishing statistics, which are needed immediately if countries of this region are to maximize economic benefits from the large skipjack resource.

Appendix

ABBREVIATIONS FOR GEOGRAPHIC REGIONS AND TIME PERIODS. Years are the survey years for which data are included in Figures 4 and 6.

CAL — New Caledonia 1977, 1978
EAST — Eastern Pacific
FIJ1 — Fiji 1978
FIJ2 — Fiji 1980
KIR1 — Kiribati 1978
NOR — Norfolk Island 1980
NSW — New South Wales (Australia) 1979
PAL — Palau 1980
PAL3 — Palau 1980
PNG2 — Papua New Guinea 1979
PON — Ponape (Federated States of Micronesia) 1979
PON3 — Ponape (Federated States of Micronesia) 1980
QLD — Queensland (Australia) 1979
SC1 — Santa Cruz Islands (Solomon Islands) 1977
SC2 — Santa Cruz Islands (Solomon Islands) 1980
SS1 — Solomon Sea (Papua New Guinea) 1977
SS2 — Solomon Sea (Papua New Guinea) 1979
SOL1 — Solomon Islands 1977
TUV — Tuvalu 1978
VAN — Vanuatu 1978
WES — Western Samoa 1978
WEST — Western Pacific
ZEA1 — New Zealand 1979

8606

Skipjack Population Dynamics; Is It Qualitatively Different from that of Other Tropical Tunas?

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Some aspects of the population dynamics of skipjack, yellowfin, and bigeye tuna are compared, and an explanation is sought for the large variations in catches of skipjack and the lack of evidence for decline in its populations following fishing. Compared with yellowfin and bigeye, skipjack is an earlier maturing species with higher natural mortality and more variable populations. It follows that its populations have fewer age classes, are more variable from changes in year class strength and availability, and have higher production/biomass ratios. Skipjack may be considered more 'r-selected' than the other tunas, i.e. the species has probably evolved for greater success in the more variable habitats of the tropical ocean through increased potential for population growth. Skipjack therefore should also be expected to be more opportunistic and migratory in comparison to the other tunas. The tropical tunas, but especially skipjack, appear to have specialized in the energy-expensive foraging strategy of sustained, fast-swimming search over large areas, and this is the likely link between their high metabolic and natural mortality rates. It is further suggested that the higher natural mortality of skipjack is more density dependent than in the other tunas, and that this reduces the effects of fishing.

Ce document fait une comparaison de certains aspects de la dynamique des populations du listao, de l'albacore et du thon obèse, et cherche à donner une explication sur les variations importantes des prises de listao et le manque de preuves du déclin de leurs populations par suite de la pêche. Le listao, comparé avec l'albacore et le thon obèse, est une espèce à la maturité plus précoce, à la mortalité plus importante, et dont les populations sont plus variées. En conséquence, ses populations présentent un nombre moindre de classes d'âge, sont plus variables en ce qui concerne les changements de l'abondance et de la disponibilité des classes annuelles, et ont un taux production/biomasse plus élevé. On peut donc considérer le listao plus "r-sélectionné" que les autres thonidés; par exemple, l'espèce a probablement évolué pour mieux s'adapter dans des habitats plus variés de l'océan tropical en augmentant le potentiel de croissance de sa population. On croit donc que le listao est plus opportuniste et migratoire que les autres thonidés. Les thonidés tropicaux, mais surtout le listao, semblent s'être spécialisés dans une technique de recherche de nourriture exigeant de gros efforts, car ils doivent continuellement se déplacer rapidement sur de grandes étendues, et ce phénomène est probablement le lien entre leurs taux élevés de mortalité naturelle et métabolique. Il est également suggéré que la mortalité naturelle élevée du listao dépend plus de la densité que celle d'autres thonidés, ce qui diminue les effets de la pêche.

Se comparan algunos aspectos de la dinámica de pobiaciones de rabil, listado y patudo, buscándose explicación a las grandes variaciones en las capturas de listado y la falta de evidencia de descenso de sus poblaciones después de la pesca. En comparación con el rabil y el patudo, el listado es una especie de maduración mas temprana, con una mortalidad natural mas alta y mayor variación en las poblaciones. Por ello, estas poblaciones cuentan con menos clases de edad, la disponiblidad y fuerza de la clase anual experimenta mas cambios y las tasas de producción/biomasa son mas altas. Se puede considerar al listado como una especie mas "r-seleccionada" que el resto de las especies de túnidos, es decir, esta especie ha evolucionado para mejor éxito en los habitats mas variables del océano tropical por medio de un incremento en el potencial de crecimiento de la población. Por lo tanto, se podría esperar que el listado sea mas oportunista y migratorio, en comparación con el resto de los túnidos. Los túnidos tropicales, en especial el listado, parecen haberse especializado en una estrategia para buscar alimento que exige grandes esfuerzos, ya que nadan continuamente por amplias zonas, siendo esta característica el posible lazo de unión entre su rápido metabolismo y sus tasas de mortalidad natural. Se sugiere también, que la alta tasa de mortalidad natural del listado depende mas de la densidad que en el caso de otras especies de túnidos y este hecho reduce los efectos de la pesca.

1. Introduction

Skipjack tuna (*Katsuwonus pelamis*) populations are remarkable in that catches in the various fisheries have risen with little or no indication of declines in stock abundance. Presently total world skipjack catches surpass those of all other tunas, including the two other important tropical species, yellowfin (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*), whose stocks have shown decline under exploitation. Typically, skipjack abundance, as indexed by catch per unit effort (CPUE), shows large fluctuations but no declining trend with increasing fishing effort. The apparent ability of skipjack to remain unaffected by exploitation prompts the question of whether the species possesses population characteristics different from those of the other tunas. The question is explored in this paper by review of the fisheries and examination and comparison of population dynamics parameters pertinent to these tropical tunas. Particular attention will be paid to natural mortality and how it might be related to, and affected by, the species' foraging methods.

2. Catch and Population Trends

Skipjack catches are second only to those of yellowfin in all the world oceans, except the western Pacific and the Indian Ocean, where its catches rank first (Table 1). The largest catches have come from the western Pacific presently the primary contributor to total world catches, and where over 500,000 mt were taken in 1978 (Table 1). Though the magnitude of skipjack catches suggests large stocks, declines from exploitation are still to be expected.

Table 1. Tropical tuna catches by ocean.[1,2]

Area and Species	1977	1978	1979	1980	1981
1. Atlantic					
East (FAO areas 27, 34, 37, 47)					
Skipjack	90946	90099	78710	93595	89014
Yellowfin	120877	111234	114540	109420	98688
Bigeye	30367	38482	31886	41244	30293
West (FAO areas 21, 31, 41)					
Skipjack	6635	3701	4457	7840	7753
Yellowfin	9866	7234	9715	9555	10012
Bigeye	5574	4881	5820	6309	7692
2. Pacific					
East (FAO areas 67, 77, 87)					
Skipjack	96056	139909	121658	139374	125258
Yellowfin	183610	170460	187630	161330	167324
Bigeye	92039	76449	81511	76291	59207
West (FAO areas 61, 71, 81)					
Skipjack	412974	531013	470034	493743	434168
Yellowfin	177427	187182	188194	211010	214736
Bigeye	51948	41472	44504	45209	37898
3. Indian (FAO areas 51, 57)					
Skipjack	30334	30432	33628	45285	41567
Yellowfin	51748	45270	37566	34851	35585
Bigeye	33722	49074	32039	31968	31867
4. Total Oceans					
Skipjack	636945	795154	537645	779837	697760
Yellowfin	543528	521380	195760	526166	526345
Bigeye	213650	210358	779837	201021	166957

[1] In MT, from FAO (1981)

[2] FAO Statistics are nominal catches and do not include sport-fishing catches. These numbers are generally less than reported in the ICCAT Statistical Bulletins, which include scientists' best estimates

In reviews of Pacific skipjack fisheries, Forsbergh (1980) and Kearny (1978) found no clear, downward trends in stock size among the various skipjack fisheries. In the long-established eastern Pacific fishery, CPUE statistics, continuous from 1960, indicated no trend in stock abundance (IATTC 1982). Though Pella and Psaropulos (1975) presented evidence for population decrease in the southern area of that the differences in variability among the species' catch fishery after adjusting for increases in fishing efficiency, the effect of exploitation on eastern Pacific skipjack remains uncertain.

Eastern Atlantic skipjack also appear largely unaffected by fishing. Skipjack CPUE indexes from the 1969–1981 surface fishery of France, Ivory Coast, Senegal, and Morocco (Fonteneau et Cayré 1983) showed no evident decline with increasing fishing effort in the expanding fleet of large purse seiners. There was also no suggestion of an upper limit to the catches, though Pianet (1980) had described a parabolic relationship between catch and effort in this fishery. There was some evidence of reduced CPUE at higher effort levels in the pole and line and the medium purse seiner fleets, but in both those fleets there has been a recent trend of decreasing fishing effort.

To compare the variability of skipjack populations to that of the other tunas, the logarithms of eastern Atlantic population indexes for large purse seiner-caught skipjack, yellowfin, and bigeye tuna (Fonteneau et Cayré 1983) were plotted against year (Figure 1). Since the same relative change in successive values shows up as the same change in such plots, regardless of the absolute magnitude of the values,

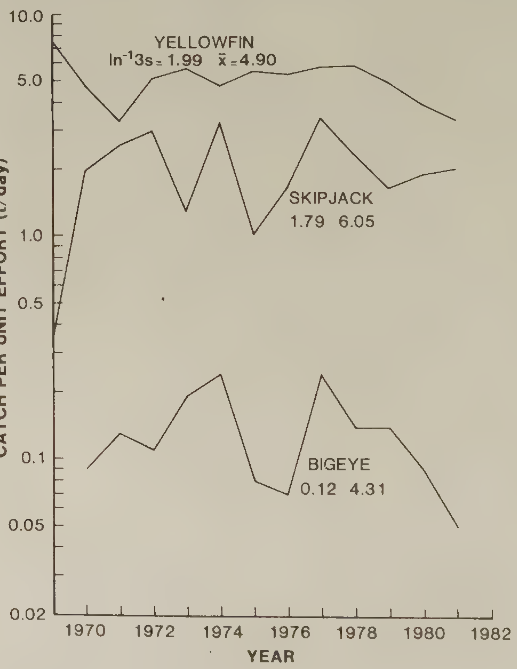

Figure 1. Catch per unit effort on logarithmic scale vs. year for skipjack, yellowfin, and bigeye tunas from the E. Atlantic large purse seiner fleet (Fonteneau et Cayré 1983). Geometric means ($\bar{x}$) and the measure of relative variability ($\ln^{-1} 3s$) are shown for each species.

rates can be compared. The population indexes of skipjack and bigeye are seen to be much more variable than that of yellowfin. Not surprisingly, bigeye tuna catch rates were highly variable, because that species is a secondary target with average catch rate that was only 7% that of skipjack. Bigeye are primarily a subsurface (deep-swimming) species.

The range in relative variability of CPUE, independent of magnitude, may be taken as

$$\ln^{-1}(3s)$$

where $\ln = \log_e$, $\ln^{-1}$ is the antilog, and s is the standard deviation of ln's (CPUE). If CPUE is approximately log-normally distributed, as is to be expected for population sizes, 3s would span about 90% of the observations, and $\ln^{-1} 3s$ would be a measure of the ratio of maximum to minimum CPUE. Values of $\bar{x}$ (geometric mean) and $\ln^{-1}(3s)$ are shown in Figure 1 for the three species of tuna. Skipjack CPUE varied 6.1 × the minumum, while yellowfin had a variability of 2.0 × the minimum. Bigeye tuna had a variability of 4.3 × the minimum.

While the yellowfin catch rates tended to decrease, the skipjack rates in the eastern Atlantic tended to increase after 1976, especially in the skipjack pole and line and medium purse seine fleets (Table 2). If the data indicate five sequential years after 1976 of above average skipjack population size, this would be unusual if the population levels were merely fluctuating randomly about the mean. The probability of a run of at least five sequential, above average years is only $(1-p)p^5 = (.5)(.5)^5 = .016$, or once in sixty-two years. This indicates that skipjack populations, while fluctuating widely, may also be sensitive to external, non-random forces.

Table 2. Tuna catch per unit effort indexes[1] from the eastern Atlantic, pole and line (P/L), medium purse seiner (MS), and large purse seiner (LS) fleets

	Skipjack			Yellowfin			Bigeye		
Year	P/L[2]	MS	LS	P/L	MS	LS	P/L	MS	LS
1969	0.40	0.84	0.35	1.52	3.78	7.50	0.18	.04	0
1970	0.60	1.31	1.98	1 06	2.35	4.72	0.13	.12	.09
1971	0.93	1.73	2.51	1.20	2.39	3.25	0.10	.07	.13
1972	0.73	1.73	2.95	1.43	2.82	5.10	0.11	.07	.11
1973	0.71	0.92	1.34	1.20	2.48	5.61	0.20	.25	.19
1974	1.00	1.95	3.22	1.39	2.47	4.73	0.13	.11	.24
1975	0.56	1.07	1.02	0.88	2.24	5.47	0.35	.09	.08
1976	0.76	0.83	1.65	1.28	2.01	5.34	0.40	.05	.07
1977	0.99	2.32	3.41	1.25	2.08	5.77	0.92	.16	.24
1978	1.20	2.03	2.34	1.01	1.62	5.81	1.28	.13	.14
1979	1.32	1.84	1.66	0.85	1.65	4.94	0.76	.14	.14
1980	1.40	2.61	1.88	0.99	3.86	3.94	1.06	.01	.09
1981	1.75	3.09	2.00	1.64	2.08	3.37	0.72	.09	.05

[1] Tons per day at sea generated by the fleets of France, Ivory Coast, Senegal, and Morocco (Fonteneau and Cayré 1983).

[2] Primary target of the pole and line fleet is skipjack

3. Vital Rates and Statistics

In this section, the vital rates of skipjack, yellowfin, and bigeye tunas are compared. Much of the data presented here were first summarized by Yoshida (1979). Instantaneous rates, where given, are expressed on an annual basis.

3.1 GROWTH

Growth in length among fishes is commonly described by the von Bertalanffy growth equation $l_t = L(\infty)(1-e^{-K(t-t_0)})$, (see Ricker 1958: 196). Table 3 summarizes recent values of the growth parameters K and L of skipjack, yellowfin, and bigeye tunas. These parameters are interrelated, but for the purpose of this paper the most important is K, which may be regarded as the rate of development of the growth pattern (Beverton and Holt 1957: 288). K estimates varied approximately from 0.3 to 1.0 for skipjack[1], from 0.3 to 0.5 for yellowfin, and 0.2 to 0.4 for bigeye. Relative to the other tunas, skipjack would seem to develop about twice as fast. This is a tentative conclusion, however, because various methods and different size ranges of fish were used in the derivation of the growth parameters. LeGuen and Sakagawa (1973) and Josse et al. (1979) strongly cautioned against uncritical acceptance and comparison of growth parameters, even when the equations using them are good predictors of observed growth.

3.2 MAXIMUM AGE AND AGE AT FIRST MATURITY

Maximum age has been estimated at 5, 8+, and 9+ years respectively for skipjack, yellowfin, and bigeye by various authors (Table 4 and references). Murphy and Sakagawa (1977) estimated maximum ages of 5, 6, and 7 years for these same species. The table suggests that skipjack have a maximum lifespan perhaps only half that of the other tunas. The age at first reproduction is approximately 1–1.5 years, as opposed to 1.5–3 and 2–3 years for yellowfin and bigeye respectively. Again, skipjack may become mature earlier than the other tunas by a factor of one-half. Since the rate of population increase depends strongly upon how early reproductive maturity is achieved (Cole 1954; Lewontin 1965), there is an increasing trend, from bigeye to skipjack, in the potential for population growth.

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[1] From Pacific growth rates. In the E. Atlantic Bard and Antoine, (this volume) studied the growth of tagged fish, finding, for $L(\infty)$ set at 80 cm, K = .332 in equatorial waters and K = .601 in north tropical waters

Table 3. Parameter estimates of the von Bertalanffy growth equation for skipjack, yellowfin and bigeye tunas.

Species	to	K	$L(\infty)$	Author	Comments
Skipjack	−0.0231	0.5483	102.04	Uchiyama and Struhsaker (1981)	Hawaii, by dialy growth rings
	−0.016	0.432	103.8	Chi and Yang (1973)	W. Pacific; by modal progression
		0.95	85.1	Joseph and Calkins (1969)	Hawaii; by modal progression
		0.431	88.1	Joseph and Calkins (1969)	E. Pacific; tag returns
		0.77	82.3	Rothschild (1967)	C. Pacific; tag returns
		0.94	65.5	Josse et al.	W. Pacific; tag returns
		0.64	79.1	(1979)	E. Pacific; tag returns
		0.52	74.8	Wankowski (1981)	W. Pacific, modal progression
		0.20	79.6	Batts (1972a)	N. Carolina, dorsal spine "annuli"
		0.32	80	Bard and Antione	E. Atlantic, equatorial; tag returns
		0.60	80	this volume	E. Atlantic, north tropical; tag returns
Yellowfin	−1.032	0.312	197.5, 190	Shomura (1966),	W. Pacific, longline, scale annuli
		0.33	190	Suzuki (1971),	
		0.32	188.4	and Le Guen and Sakagawa (1973) resp.	
	0.267	0.454	190.2	Shomura (1966),	Hawaii, mainly longline,
	0.22	0.440	192	Suzuki (1971),	weight frequency
		0.430	191.9	and Le Guen and Sakagawa (1973) resp.	
	0.86	0.60	169	Hennemuth (1961),	E. Pacific, mainly baitboat,
	0.47	0.36	203.3	Le Guen and Sakagawa (1973)	length frequency
	0.83	0.60	167	Davidoff (1963)	E. Pacific, mainly baitboat length frequency
		0.36	195.2	Yang et al (1969)	W. Pacific, longline, scale annuli
		0.28	222.8	Yang et al (1969)	E. Atlantic, longline, scale annuli
		0.28	223.0	Le Guen and Sakagawa (1973)	
	0.52	0.3828	191.7	Le Guen et al. (1969)	E. Atlantic, length frequency
	0.62	0.42	194.8	Le Guen and Sakagawa (1973)	E. Atlantic surface fisheries, length frequency
		0.5568	165.8	Le Guen et	E. Atlantic (Pointe Noire), length frequency
		0.5418	166.5	Champagnat (1968)	
		0.4308	182.3	Le Guen et Champagnat (1968)	E. Atlantic (Dakar), length frequency
Bigeye	0.00055	0.208	215	Yukinawa and Yabuta (1963),	Pacific, scale annuli
	0.017	0.212	213.1	Shomura (1966)	
	0.528	0.38	186.95	Kume and Joseph (1966)	E. Pacific, length frequency
	−1.128	0.16	195.2	Shomura (1966)	Pacific, scale annuli
	−.929	0.27	196.7	Shomura and Keala (1963)	Central Pacific, longline, males, length frequency
	0.718	0.32	183.0	Shomura and Keala (1963)	Central Pacific, longline, males, length frequency

Table 4. Life span and reproductive age estimates for skipjack, yellowfin and bigeye tunas.

Species	Ages in Fishery: Surface	Subsurface (longline)	Max. age	Age at first reproduction
Skipjack	1–3	——	4–5[1]	1–1.5 years[2]
Yellowfin	1–5[3]	2–6+[4]	8+[5]	1.5–3 years[6]
Bigeye	1–4[7]	2–7+[8]	9+[9]	2–3 years[10]

[1] Approximate age of 850 mm fish (see Shomura (1966))

[2] 400–450 mm fish; growth curves of Uchiyama and Struhsaker (1981), Joseph and Calkins (1969)

[3] Honma and Suzuki (1978), Cole (1980), Hayasi and Honma (1971)

[4] Shingu et al. (1974), Hayasi and Honma (1971), Honma et al. (1971)

[5] Hayasi and Honma (1971)

[6] Kikawa (1962), Orange (1961), Ueyanagi (1966), Yuen and June (1957)

[7] Kume and Joseph (1966)

[8] Sakamoto (1967), Kume (1967)

[9] Sakamoto (1967)

[10] Calkins (1980), Kume and Joseph (1966), Kikawa (1962), Kume (1967)

3.3 NATURAL MORTALITY

Natural mortality rate perhaps gives the most insight into the population dynamics of species. It is also the most difficult parameter to estimate. Most measures of the instantaneous natural mortality rate, M, for tunas have been obtained from studies of yellowfin (Table 5). Indeed the value of 0.8 for yellowfin by Hennemuth (1961) is something of a standard in tuna population dynamics, even though his sample was from the pole and line fleet, where larger (older) individuals were probably under-represented. Studies of primarily long-line caught yellowfin, where emigration was considered, have suggested lower rates (Honma et al. 1971, Ishii 1969, Hayasi and Honma 1971). A population model by Francis (1977) of the eastern Pacific surface yellowfin fishery had better correspondence to observed dynamics when M was set at 0.6. There are only a few estimates of M for bigeye tuna. They range from 0.35 to 0.68, and are similar to those of yellowfin (Table 5).

There are also few estimates of skipjack natural mortality, and a value of 0.8, as in yellowfin, is often assumed. Murphy and Sakagawa (1977) considered skipjack M to be between 0.69 and 0.93, on the basis of the relationship between M and the growth constant K (Table 5). The difficulty with this and similar correlations is that the variables may already be correlated through the estimates of age. This is because, as Beverton and Holt (1959) noted, age span in fishes appears adjusted to the time needed to complete the growth pattern.

Although natural mortality must be inversely related to age span, there is no simple way of deriving M from estimates of maximum age (t_{max}). In the presence of mortality there is not a simple relationship between maximum age and mean age; it is the latter that is actually inversely related to M. Mean age is not a firm statistic, especially for skipjack. If natural

Table 5. Estimates of instantaneous natural mortality (M) for skipjack, yellowfin and bigeye tunas

Species	M/year	Author	Comments
Skipjack	3.00	Bayliff (1977)	tagging data; uncertain reliability
	1.68	Joseph and Calkins (1969)	tagging data; uncertain reliability; emigration, etc. losses included
	0.69–0.93	Murphy and Sakagawa (1977)	from relationship between M and K (of von Bertalanffy equation)
Yellowfin	0.64–.80–.92	Hennemuth (1961)	E. Pacific 1955–59, primarily baitboats
	0.55–1.05	Schaefer (1967)	Revision of Hennemuth (1961)
	1.2	Honma et al. (1971)	C. and W. Pacific; high values (1971) suggested as possibly due to emigration at ages 3.5+
	0.44	Ishii (1969)	Pacific; all-age average; emigration accounted for
	0.3–0.8	Hayasi and Honma (1971)	Summary of several Japanese studies
	0.35–0.44	Kawakami and Kitahara (in Suda 1971)	Indian Ocean
	0.60	Francis (1977)	From model simulating E. Pacific surface fishery
Bigeye	0.35–0.56	Ishii (1968)	Pacific; simulation model of fishery
	0.36	Suda and Kume (1967)	Pacific; age 6 and longline caught fish
	0.44–0.68	Murphy and Sakagawa (1977)	Relationship between M and K (of von Bertalanffy equation)

mortality of the exponential type were acting alone upon an adult population, where youngest age was t_a, we could obtain M as:

$$M = 1/(\bar{t}-t_a)$$

where $\bar{t}$ = average age. The average age should fall between t_a and $(t_{max}-t_a)/2$ (the latter e.g. in the unlikely case that mortality was zero in the interval). If t_a were set at 1 year and t_{max} at 5, 8, and 9 years (see above) for skipjack, yellowfin, and bigeye respectively, the range for $\bar{t}$ would be 1–2, 1–3.5, 1–4.0 years respectively. Even within this restricted range, the possible values of $\bar{t}$ lead to sets of calculated M too imprecise to be useful.

The idea that M is constant throughout the adult life of fish is largely an assumption, but consistent with the observation that animals without notable learning, and subject mainly to random accidents or predation, tend to die at a constant rate. Bird survivorship curves are the classic examples of this pattern. However, in a review of survivorship among various vertebrates, invertebrates, and plants, Hutchinson (1979) found a variety of mortality patterns, depending less upon classification than upon the relative vulnerabilities of juvenile, adult, and senile stages, and the abruptness of the transition between the stages. In this regard one should note that fish, unlike birds, grow to many times over their initial adult weight, skipjack over four times and yellowfin and bigeye over ten times between ages 1 and 2 years. Finally, an age constant M might not be expected if natural mortality in tropical tunas is due to the cost of obtaining sufficient food rather than directly to predation.

3.4 M AND METABOLIC RATE

The apparent high natural mortality rate of tropical tunas may be puzzling, considering the relatively large size and great locomotory power of these fish. An M of 0.8 that is often assigned to yellowfin is in the upper range of natural mortality among commercial species that grow > 50 cm (e.g. Beverton and Holt 1959). It seems likely, though, that the high natural mortality of tunas is associated with their high metabolic rates.

The metabolic, digestive, and respiratory rates of tropical tunas may be the highest among all teleosts (Magnuson 1978, Stevens 1972, Gooding et al. 1981). Kitchell et al. (1978) explained how physiological limits to the ability to process food, together with high metabolism, could result in increasingly reduced energy for growth in larger skipjack. One would therefore expect increasing natural mortality rate among older fish. Comparing survivorship, one notes that unlike skipjack, yellowfin and bigeye survive to form fishable populations of older fish at deeper and cooler depths. Their retention of the gas bladder into adulthood, adaptive if feeding excursions from depths to the surface are no longer frequent, and their lower natural mortality indicate an adaptive departure from the skipjack condition (Sharp 1978).

The general relationship that smaller, shorter-lived (higher M) species have higher metabolic and population increase rates, while larger species show the opposite tendency (Bonner 1965; Fenchel 1974) is consistent with the correlation of M and higher metabolism. Bourliére (1957) reviewed experiments performed on both vertebrates and invertebrates and concluded there was a negative relationship among and within species between metabolic rate and lifespan. Evidence that reproductive activity decreases adult survival and growth while increasing energy expenditure in fish and other animals was summarized by Stearns (1976). Priede (1977) described a model relating increased natural mortality to increased time spent in high energy activity. The link between metabolic rate and M is further supported by the significant correlation between M and water temperature in fishes (Pauley 1980). His compilation of evidence showed that for fish growing > 50 cm, M > 0.8 is often reported among tropical species.

3.5 METABOLISM AND FORAGING STRATEGY

It seems that a high metabolic rate developed in the tropical tunas to meet the requirements of an energy-expensive foraging strategy. The external morphology and behavior of these tunas suggests that this strategy is sustained, fast-swimming search for sparsely distributed food over large areas. The development of this ability doubtlessly played an important role in making it possible for these tunas to expand into the relatively unproductive, offshore tropical ocean. The selective pressure involved can be appreciated by considering the probability P(x) of encountering food items or patches by random searching in a horizontal plane. In search theory (Koopman 1956), the distance x required to achieve a certain cumulative probability P(x) of encountering a randomly distributed target is

$$x = \frac{-\ln[1-P(x)]}{k}$$

where k is the instantaneous probability of detection in a small distance interval dx. Since the numerator is a constant for a given P(x), any reduction in k, e.g. due to lowered average density of food, requires a disproportionate increase in search distance x (and energy expenditure) according to a hyperbolic relationship, the effect being stronger for larger P(x) (Figure 2). The short-lived skipjack are apparently faster and more far-ranging than the other tropical tunas (Kearney 1978), indicates a strong specialization in this direction. Their abundance, even in the relatively unproductive, deep-mixed layers of the central and western tropical oceans (Forsbergh 1980; Kearney 1978), indicates the species' success. However, the cost of this specialization seems to be natural mortality more severe than in the other tropical tunas.

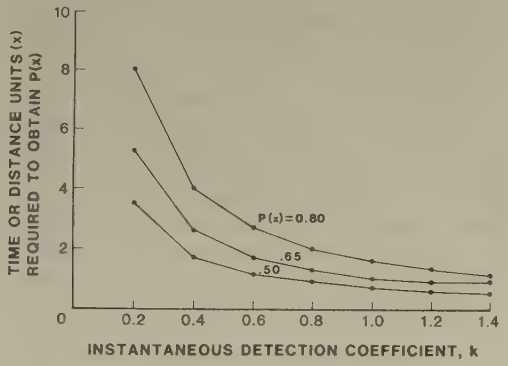

Figure 2. Hypothetical example illustrating the change in time or distance required for successful search (i.e., obtaining P(x) in some unit of time) as a function of the instantaneous detection probability or coefficient, k. P(x) is the cumulative probability of intercepting food after x time or distance units. k can be considered a measure of the average density of food in the environment being randomly searched. See text.

3.6 Production and Critical Age

The leading role of tunas in tropical ocean fisheries is due to their high productivity and large habitat, roughly the entire tropical and subtropical ocean. These fish are productive not in spite of their high natural mortality, but as a correlate to it. Allen (1971) showed that for exponential mortality and von Bertalanffy growth (as well as several other growth models), the production/biomass ratio over a cohort's life is equal to its (constant) mortality rate. Over shorter periods, during which growth may be considered exponential, this ratio is equal to the instantaneous growth rate. From Table 5 estimates of M for skipjack, yellowfin, yellowfin and bigeye might be e.g. 1.0, 0.7, and 0.5 respectively, so that the production/biomass ratio of skipjack could be 43% and 67% larger, respectively, than that of yellowfin and bigeye tuna.

It is useful, too, to look at the instantaneous growth rate, $g = \log(w_{t+1}/w_t)$, relative to M, to determine the critical age or size of individuals in a cohort, i.e. when $g = M$ and the cohort's biomass is largest. Figure 3 shows that the weight specific or instantaneous growth rate is less at a given age for the smaller skipjack in comparison to yellowfin and bigeye, and that the critical age is 1–1.5 years for skipjack, about 2 years for yellowfin, and 2.5–3 years for bigeye. The yield per recruit (Y/R) consideration of fishery population dynamics seeks to determine the harvest at the critical age, but under a practical exploitation schedule over several ages. With few significant age classes in skipjack populations, and the low critical age, it is clear that increases in Y/R of this fish would accrue mostly from increasing fishing mortality, not from increasing age at entry to the fishery.

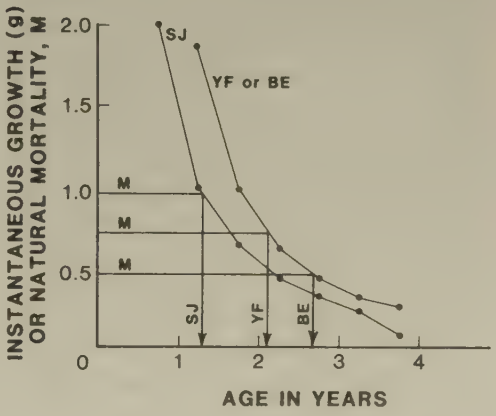

Figure 3. Instantaneous growth rate, g, vs. age as calculated for skipjack, yellowfin, and bigeye. Critical age is indicated by arrows, defining condition where g = natural mortality, M. Growth equations are by Joseph and Calkins (1969) and Hennemuth (1959b) for skipjack, Chatwin (1959) and Le Guen and Sakagawa (1973) for yellowfin, and Kume and Joseph (1966) and Morita (1973) for bigeye.

4. Discussion

This review of skipjack population characteristics indicates that the species may develop about twice as fast and mature twice as early as yellowfin and bigeye. Its natural mortality may be near 1.0 yr^{-1}, which would make its production/biomass ratio perhaps 43% greater than that of yellowfin. In these respects skipjack are "r-selected" relative to yellowfin and bigeye. This term does not strictly refer to the parameter r but rather to a type of survival strategy (see Southwood et al. 1974). As such, skipjack should be more opportunistic, productive, and migratory, and more affected by environmental changes. The species seems qualitatively different in this context.

Skipjack are notable in being composed of only two or three significant age classes that support surface fisheries only. This simple population structure can exacerbate effects of fluctuations in year-class strength. If R is the average annual recruitment, the average fraction of a stock at equilibrium comprised of first year fish is $[R(1-e^{-M})/M]/[R/M] = 1-e^{-M}$ (Ricker 1958: 28). If $M = 1.0$, on average 63% of the stock will be of the incoming year class. Therefore, abundance indexes will be strongly affected by year class fluctuations and, until recruitment is affected, it may be difficult to see the effects of fishing. The extensive movements of the species must also contribute to fluctuations in availability to the fishery, and this too will make analysis of population structure difficult. The range of fish size available to the fishery at any particular time seems especially variable in skipjack, giving length-frequency modes that are erratic and short-lived. This is the basic reason why it is difficult to measure mortality rates in this species.

An interesting hypothesis from modern population theory is that species with intrinsic rates of increase greater than 2.0 year^{-1} can be induced to exhibit stable, or even "chaotic," fluctuations of population size, basically because of strong overcompensation of population response to changes in density (May et al. 1974; May 1976). While the intrinsic rate of increase, r, for skipjack cannot be estimated with confidence because of poor understanding of net reproductive rate and mean generation length, one can note that r is probably much less than 2.0. Even if it were twice that of the Pacific sardine, whose r was estimated as 0.34 by Murphy (1967), the intrinsic rate of increase of skipjack, and probably most commercial fish, would be far below 2.0. This is the reason why even productive fish species can be fished down to levels where recovery is impaired. In contrast, many other animals, e.g. small rodents with mean generation lengths less than one year, have r's greater than 2.0 (Caughley 1977: 112), and their recovery from "overfishing" is virtually assured, and a recurring problem. One must conclude, therefore, that population fluctuations of skipjack are primarily direct responses to external perturbations affecting survival, rather than to sustained oscillations.

An erratic population size and yield will induce a fishery to focus on short-term exploitative goals that are also consistent with recommendations that would come from standard population analyses. Provided that fishing does not impair reproductive potential, skipjack fishing should be as intense as practical.

Most features of skipjack populations appear to be consistent with what might be predicted from the comparison of population dynamics parameters among the three important tropical tunas. However, the comparison did not lead to an explanation of why skipjack appear so unaffected by exploitation. The question remains of how a population, such as that of the eastern Atlantic skipjack, can continue to support catches of over 100,000 mt per year and not show clear evidence of decline. There are at least two possibilities:

1) There is a decline, but it is not detectable in the overall CPUE statistics because of large variability in the resource or its availability or because of changes in fishing efficiency. Skipjack populations may be so variable that underlying population trends cannot yet be detected, or so productive and widespread, relative to the fisheries, that the latter have local effects only, i.e. the fisheries have not yet subjected entire stocks to significant exploitation. This argument may be applicable to eastern and western Pacific skipjack resources, but is less credible in the Atlantic, where the major fishery is in the Gulf of Guinea and the stock presumably smaller, but still without clear evidence of decline. With respect to increased fishing efficiency, the catchability (q) of schools from reduced populations could have increased so as to mask the evidence for decline. However, this seems unlikely to be an important factor in skipjack, considering the species' extensive habitat and high mobility.

2) The high natural mortality of skipjack may actually decrease under exploitation. First, skipjack must compete to some extent with yellowfin and bigeye tunas so that reductions in the latter tunas may be beneficial. If skipjack are the more opportunistic, i.e. "r-selected," of these tunas, it would be the species most likely to respond positively when simultaneous reductions in population size of these fishes occur. Second, and I think more likely, skipjack natural mortality may actually decrease under exploitation from intraspecific, density dependent effects that are a function of the foraging behavior. The probability of not encountering adequate food may increase in large schools that may be more common in lightly exploited stocks. Fish so disadvantaged may weaken rapidly, swim less strongly, and suffer further reduction in their food encounter rate. Similar difficulties are faced by certain stream dwelling fishes that must swim into the current, holding position there in order to ensure adequate food. Juvenile salmonids, for example, obtain their drifting food by maintaining position in preferred locations, either directly in the current or in the eddies, depending upon stream velocity (Symons 1976). Those fish unable to station themselves in positions of adequate food-flow become weaker, fall behind to less advantageous sites, and suffer a higher mortality that is density dependent (Au 1972).

The important feature of density dependent natural mortality is that fishing mortality can compete with it, rather than simply add to it. As a result, total mortality (natural + fishing) could change little as fishing effort is increased. For example, the total mortality rates (Z) of exploited eastern Pacific skipjack have apparently not increased with increasing fishing effort (Table 10 in IATTC 1982). Kearney (1978) proposed that skipjack were subject to large fluctuations in natural mortality to explain the large annual fluctuations in catches from the western Pacific. I suggest that changes in natural mortality may be density dependent and that this feature is more strongly developed both in developmental stages and in species that have high natural mortality.

Density dependent, high mortality is a feature of the larval and juvenile stages of many fish. It probably is the mechanism whereby many marine fishes exhibit no trend in average numbers of recruits over wide ranges of population size (Harris 1975; Beverton and Holt 1957: 51). The above hypothesis on adult skipjack natural mortality is not supported by data, but if correct, then skipjack may be considered a tuna that, with respect to natural mortality, has largely remained at the juvenile stage.

This paper has emphasized the importance of natural mortality as an indicator of a number of aspects of population biology. Unfortunately we know little about this mortality and estimates of its value are imprecise. Studies focused on individual fish could contribute much to understanding how natural mortality is affected by age and population density. Learning about the condition or fatness of tunas of different sizes, from different areas, from schools of different sizes, and from different locations within a school, would help test and develop hypotheses about mortality.

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SEABIRD INTERACTIONS WITH DOLPHINS AND TUNA IN THE EASTERN TROPICAL PACIFIC[1]

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Abstract. Bird flocks associated with dolphins in the eastern tropical Pacific are described from observations obtained during eight cruises that took place from January to March of 1976, 1977, 1979, and 1980. In the northern tropical waters between latitudes 5°N and 30°N, 43% to 53% of bird flocks co-occurred with dolphins. In equatorial and southern subtropical waters between latitudes 5°N to 12°S and in the central Pacific less than 8% of the flocks were associated with dolphins. In northern tropical waters about 70% of dolphin schools associated with flocks were composed of spotted or spotted plus spinner dolphins; conversely, 59% of spotted dolphin and 96% of spotted plus spinner dolphin schools co-occurred with bird flocks. Most large schools of these dolphins were associated with birds, and the number and diversity of bird species increased with dolphin school size. The average species composition of birds in dolphin-associated flocks of northern tropical waters was: boobies 41.7%, Wedge-tailed Shearwaters (*Puffinus pacificus*) 31.4%, jaegers 12.8%, Sooty Terns (*Sterna fuscata*) 6%, frigatebirds 3.6%, and others 4.5%. Positive statistical associations were found among these bird species, which are explained by common attraction to food made available by feeding yellowfin tuna. In the southern latitudes and in the central Pacific, flocks were dominated by Sooty Terns, and few flocks were associated with dolphins. These flocks appeared to be associated with skipjack rather than yellowfin tuna.

Key words: *Foraging interactions; tropical seabirds; tuna; dolphins; Pacific Ocean.*

INTRODUCTION

Flocks of seabirds accompanying dolphin schools (order Cetacea) are a conspicuous sight in the eastern tropical Pacific (ETP). Tuna fishermen search for these flocks to locate dolphin schools and the yellowfin tuna (*Thunnus albacares*) that swim with them. These flocks are usually associated with only a few of the many species of dolphins found in the ETP. It is only those few dolphin species, in turn, that are commonly associated with tuna. The dolphin-associated tuna are primarily yellowfin and, less frequently, skipjack *Katsuwonus pelamis* (Hammond 1981). In this paper, we describe the characteristics of seabird flocks that associate with dolphins and also describe the nature of the joint aggregations of birds, dolphins, and tuna. We present evidence for a major discontinuity in the pelagic community—between multispecies flocks associated with dolphins and yellowfin tuna, on the one hand, and single species flocks associated with small tuna, on the other.

METHODS

Our seabird observations began in 1976 during cetacean surveys carried out by the Southwest Fisheries Center. The main surveys jointly used NOAA ships *David Starr Jordan* and *Townsend Cromwell* during each January through early March of 1976, 1977, 1979, and 1980; the combined eight cruises broadly sampled the main yellowfin tuna fishing grounds in the eastern Pacific (Fig. 1). These grounds, described by Calkins (1975), lie roughly within the triangular area whose base is formed by the American coasts between latitudes 25°N and 15°S and whose apex is offshore at latitude 10°N, longitude 150°W.

Though the main purpose of the surveys was to determine the distribution and relative abundance of the different cetacean species, especially the dolphins that interact with the tuna fishery (Au and Perryman 1985), sightings of birds were also recorded. During daylight hours the sea surface was searched continuously while ships were underway, using two pairs of 20 or 25 power binoculars mounted port and starboard on or above each ship's bridge. We watched for bird flocks because of their association with cetaceans and also for independent avian studies. All observed species and numbers of birds were recorded. Because large flocks were difficult to enumerate, the counts are our best estimates. Although individual species of both birds and cetaceans differ in conspicuousness, possible biases in species counts are mitigated in this study by focus on the more carefully observed dolphin-associated flocks. When a cetacean school and/or bird flock was sighted, the ship approached it and usually passed through the aggregation. In this way we obtained close-up observations of species composition and behavior of the bird flocks and of the cetaceans. The distance to the horizon was 10.2 to 13.0 km, depending

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[1] Received 20 August 1985. Final acceptance 4 February 1986.

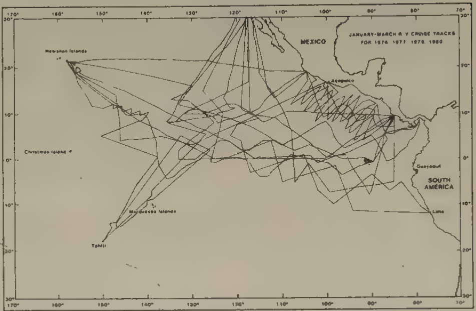

FIGURE 1. Research cruise tracks along which bird observations were taken.

upon the height of the observer's eye above the sea surface.

In this paper we discuss bird observations from the research cruises in 1977, 1979, and 1980 (13 cruise months). This data set was obtained with better areal coverage and species identifications than in 1976. Information from other, shorter research cruises (11 between 1976 and 1981) was also used.

We divided the data into two latitude intervals: 5°N to 30°N and <5°N to 12°S. The northern interval enclosed northern tropical (NT) waters and the southern interval the equatorial and southern tropical and subtropical (ESTS) waters surveyed. These oceanographic water types were defined by Wyrtki (1967); Ashmole (1971) discussed the seabirds, and Au and Perryman (1985) discussed the dolphins associated with these water types. Briefly, NT waters are the warm (>25°C), low salinity (<34‰) waters of the Equatorial Counter Current and the southern portion of the North Equatorial Current. Seasonal changes in NT characteristics are relatively small. The ESTS waters lie along the equator (equatorial water) and extend southward into the southern ocean (southern subtropical water). ESTS waters are seasonally variable, affected by upwelling, extensions of the Peru Current, and large seasonal changes in weather. The data are presented here with respect to the two latitude intervals to show the broad patterns of bird-dolphin interactions that are related but not restricted to the specific water types in each interval.

Characteristics of bird flocks, the composition of species in the flocks, and their degree of association with species of cetacea are described from the counts of individuals of each species. Aggregations of more than 10 birds were considered to be flocks; fewer birds were often too scattered to be described as a flock. The species composition of flocks associated with dolphins is described from the counts of all birds found with the dolphins. Association among these bird species was ascertained using Chi-square tests of 2 × 2 presence-absence tables of species in the flocks (e.g., Pielou 1969).

RESULTS

FLOCK CHARACTERISTICS AND CO-OCCURRENCE WITH DOLPHINS

The species composition of flocks, as well as the proportion of flocks associated with cetaceans, varies by area. Table 1 gives the aggregate data for the main species that make up these flocks, regardless of whether the flocks were associated with cetaceans. In addition to the NT and ESTS latitude intervals, the data are also classified according to two main longitude (zonal) intervals that we call the eastern Pacific (Central America to longitude 125°W) and the central Pacific (longitude 125°W to 155°W). Most avian species or groups were proportionately less abundant in flocks from central Pacific and ESTS waters than in flocks from NT waters of the eastern Pacific. The terns were a notable exception to this trend; in particular, Sooty Terns (*Sterna fuscata*) increased in the eastern Pacific from 15.1% of total birds in NT waters to 62.2% in ESTS waters, while in the central Pacific they increased from 63.5% in NT waters to 79.4% in ESTS waters.

Bird flocks that co-occurred with cetaceans were associated primarily with delphinids, in particular certain dolphins. But whereas less than 8% of flocks were with these dolpins in central Pacific and ESTS waters, the percentage of flocks with dolphins averaged 43% to 53% in NT waters of the eastern Pacific (Table 2). The 53% pertains to a coastal belt about 1,100 km wide off Central America, which was surveyed intensively in 1979 (see Fig. 1). Flocks were rarely seen with whales, even off Central America.

Dolphin-associated flocks were significantly larger than those not associated with dolphins. In NT waters the geometric mean of flock size (appropriate because flock size distribution tends to be skewed) increased from 27.3 birds (95% confidence interval 24.4–30.5) in flocks without dolphins to 57.0 (95% CI 47.7–68.1) in flocks with dolphins. In ESTS waters mean flock size increased from 29.1 in flocks without dolphins (95% CI 26.3–32.2) to 43.4 in flocks with dolphins (95% CI 36.3–51.9).

SPECIES OF DOLPHINS ASSOCIATED WITH BIRD FLOCKS

Seabird flocks regularly associated with only 5 dolphin species out of at least 23 species of cetaceans, including whales, found in the ETP. The degree of association varied greatly among these 5 species of dolphins. In both NT and

TABLE 1. Major species in flocks with ≥10 birds, eastern vs. central Pacific.[1]

Bird species	Eastern Pacific coast–125°W				Central Pacific[2] 125°–155°W			
	5°N–30°N		<5°N–12°S		5°N–30°N		<5°N–12°S	
	n	%	*n*	%	*n*	%	*n*	%
Booby spp. *Sula sula,* etc.	9,774	34.27	2,490	15.26	161	0.40	751	0.47
Wedge-tailed Shearwater *Puffinus pacificus*	7,146	25.03	293	1.80	447	11.27	249	1.57
Sooty Tern *Sterna fuscata*	4,300	15.06	10,153	62.21	2,519	63.50	12,567	79.37
Jaeger spp. *Stercorarius* spp.	2,686	9.41	88	0.54	116	2.92	28	0.18
Noddy/other Terns *Anous, Chlidonius, Gygis* spp.	1,984	6.95	2,618	16.04	6	0.15	2,254	14.24
Frigatebird *Fregata* spp.	1,050	3.68	303	1.86	9	0.23	146	0.92
Other shearwaters *Puffinus lherminieri, P. auricularis, P. nativitatus,* etc.	1,179	4.13	28	0.17	104	2.62	11	0.06
White-necked/Juan Fernandez/Dark-Rumped petrels *Pterodroma externa, P. phaeopygia*	309	1.08	319	1.95	692	17.44	259	1.64
Other gadfly petrels *Pterodroma* spp.	118	0.41	29	0.18	58	1.46	245	1.54
Totals	28,546	100	16,321	100	3,967	100	15,834	100

[1] From January–March cruises, 1977, 1978, 1980.

[2] From total counts taken aboard R/V *Townsend Cromwell.* Data from near Marquesas, Tuamotu, and Society islands excluded.

ESTS waters, spotted (*Stenella attenuata*) and spinner (*S. longirostris*) dolphins co-occurred most frequently with flocks; 58.9% and 52.9% respectively of these dolphins' schools were associated with flocks in NT waters (Fig. 2, top). These two dolphin species often occur together (approximately one third of spotted dolphin schools are found mixed with spinner dolphins [Au and Perryman 1985]); 96.4% of such mixed schools were with bird flocks in NT waters. In those same waters 30.6% of common dolphin (*Delphinus delphis*) schools were with flocks, and only 12.5% of rough-toothed dolphin (*Steno bredanensis*) and 1.6% of striped dolphin (*Stenella coeruleoalba*) schools were with flocks. Notice that the percentage of schools of the above dolphin species that were associated with birds decreased markedly in ESTS waters compared with NT waters.

We measured the relative likelihood of a particular dolphin species being found in any given bird-dolphin aggregation as the percent of all dolphin-associated bird flocks that co-occurred with each dolphin species or group (Fig. 2, bottom). Of the above five dolphin species, spotted and mixed spotted plus spinner dolphin schools were the most likely (35.9%

TABLE 2. Percent of flocks (≥10 birds/flock) with cetaceans.

Area	Latitude	Flocks	w. Delphinids[a]			w. Whales		
			n	%	Range[b]	*n*	%	Range[b]
1. Eastern Pacific								
Entire	5°N–30°N	363	155	42.7	36.4–52.1	5	1.4	1.1–1.6
Off Cent. Amer.	5°N–30°N	256	135	52.7	48.0–75.9	4	1.6	0–2.6
Off Cent. Amer.	<5°N	344	26	7.6	4.3–33.3	3	0.9	0–2.0
2. Central Pacific	5°N–30°N	76[c]	3	3.9[d]	—	0	0	—
	<5°N	305[c]	1	0.3[d]	—	0	0	—

[a] Includes dolphins and certain small "whales," e.g. pilot whale.

[b] Range among cruises.

[c] Data based on *Townsend Cromwell* cruise 77-1; flocks based upon flock counts of *Sterna fuscata* only

[d] Maximal estimates

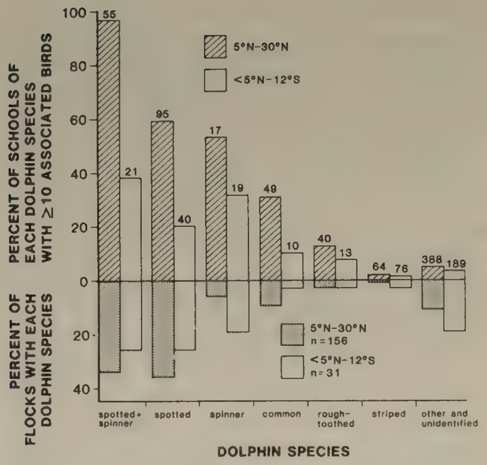

FIGURE 2. The percent of dolphin schools of each species or species group with bird flocks (upper) and the percent of all dolphin-associated flocks with each species or species group of dolphins (lower). Numbers over the bars are the schools examined. "Other and unidentified" category probably includes many spotted and spinner dolphin schools.

and 34.0%, respectively) and the striped dolphin least likely (0.6%) to be present in bird-dolphin aggregations. The spinner dolphin, in unmixed schools, was relatively more likely to be found in such aggregations in ESTS waters than in NT waters. In part because most spinner schools with birds in NT waters were also with spotted dolphins. Common dolphins were more likely to occur in bird-dolphin aggregations in the northern latitudes.

EFFECTS OF SIZE OF BIRD FLOCKS AND OF DOLPHIN SCHOOLS

The size of bird flocks associated with dolphins tended to increase with the size of the dolphin schools. In both NT and ESTS waters the correlation between school size and flock size was positive (NT waters: $r = 0.308$, $n = 133$, $P < 0.01$; ESTS waters: $r = 0.317$, $n = 42$, $P < 0.05$).

There was a marked difference in this relationship, however, between the northern and southern waters, most apparent among the spotted and spinner dolphins either in single or mixed species schools (Fig. 3). In NT waters these schools increasingly co-occurred with flocks of 10 to 50, or with 50 or more birds as school size increased. All schools larger than 256 animals were associated with flocks of at least 10 birds (school size interval is plotted on a logarithmic scale). In contrast, most of such schools in ESTS waters were without flocks, and the frequency of schools co-occurring with flocks increased only gradually as school size increased.

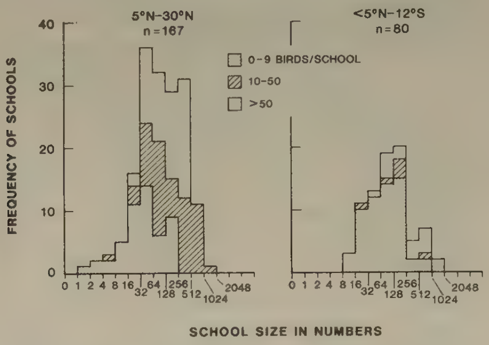

FIGURE 3. Effects of school size (spotted and/or spinner dolphins only) on the frequency of schools with bird flocks.

The average size of bird flocks varied with the species of dolphin. The largest flocks co-occurred with spotted and mixed spotted plus spinner schools (Table 3). As flocks associated with these dolphins increased in size, the number of birds of each species also increased. This was especially evident for boobies (*Sula* spp.), Wedge-tailed Shearwaters (*Puffinus pacificus*) and jaegers (*Stercorarius* spp.) in NT waters and for Sooty Terns and boobies in ESTS waters (Table 4). At the same time, the average number of bird species per flock increased from 3.4 to 5.9 as flock size increased from less than 50 to greater than 150 birds (Table 4).

THE SPECIES OF BIRDS IN DOLPHIN-ASSOCIATED FLOCKS

In NT waters, flocks associated with spotted and/or spinner dolphins consisted of 41.7% boobies, 31.4% Wedge-tailed Shearwaters, 12.8% jaegers, 6% Sooty Terns, 3.6% frigatebirds (*Fregata* spp.), and 4.5% other species (Fig. 4). The boobies were primarily Red-footed (*S. sula*) and Masked (*S. dactylatra*), but also included Brown (*S. leucogaster*) and a few Blue-footed (*S. nebouxii*). Frigatebirds included both Great (*F. minor*) and Magnificent (*F. magnificens*); jaegers were primarily Pomarine (*Stercorarius pomarinus*), and to a lesser extent, Parasitic (*S. parasiticus*). In ESTS waters only boobies (50.2%) and Sooty Terns (32.1%) were significantly associated with spotted and/or spinner dolphins, although they did not usually occur in the same flocks. Most Sooty Tern flocks there were not associated with any species of dolphin (see Tables 1 and 2).

Among the 20 bird flocks that co-occurred with unmixed spinner dolphin schools, Wedge-tailed Shearwaters, Sooty Terns, and White-necked(WN)/Juan Fernandez(JF)/Dark-rumped(DR) Petrels (*Pterodroma externa cervicalis*/*P. e. externa*/*P. phaeopygia*), and boobies were most numerous, in that order, in

TABLE 3. Seabird species associated with five dolphin species. n = total birds; % n = % bird sp. composition; f = total flocks; n/f = mean size of sp. flocks; F = flocks associated with a dolphin sp.; % f/F = % of flocks containing a bird sp.

1. 5°N–30°N
Dolphin spp.:

	Spotted or spot. + spin.		Spinner alone		Common		Striped		Rough-toothed		All dolphins				
Flocks (F): Schools:	134 150		11 17		23 49		6 64		17 40		190 320				
Bird spp.	*n*	f	*n*	f	*n*	f	*n*	f	*n*	f	*n*	% *n*	f	*n*/f	% f/F
Sooty Tern	955	57	77	7	110	5	4	2			1,146	6.3	71	16.1	37.4
Noddy Tern	175	7			15	1	4	1			194	1.1	9	21.6	4.7
Other terns	161	18			57	4	12	2			230	1.3	24	9.6	12.6
RFB + booby[a]	5,583	101	53	3	122	12	7	2	62	8	5,827	32.0	126	46.2	66.3
Brown Booby	1,130	26	7	2	2	2			13	3	1,152	6.3	33	34.9	17.4
Msk/Bf booby	371	46	3	2	17	7	1	1	9	5	401	2.2	61	6.6	32.1
Frigatebird	617	90	3	2	90	8	1	1	22	13	733	4.0	114	6.4	60.0
WTSW	5,184	82	202	7	114	10			32	6	5,532	30.4	105	52.7	55.3
Other shearwaters	237	41			194	3	7	2	26	4	464	2.5	50	9.3	26.3
WN/JF/DR petrels	87	18	60	7	103[b]	2	1	1			251	1.4	28	9.0	14.7
Other pterodromas	12	7			3	1			10	1	25	0.1	9	2.8	4.7
Storm-petrels	29	6			3	2			6	1	38	0.2	9	4.2	4.7
Jaeger spp.	2,168	78	29	4	6	5			9	6	2,212	12.1	93	23.8	49.0
Gull spp.					2	2					2	0.01	2	1.0	1.0
Tropicbird	1	1	3	2			1	1			5	0.02	4	1.2	2.1
Other			1	1							1	0.01	1	1.0	0.5
Total	16,710		437		838		37		189		18,213				
Mean flock size[c]	41.6		19.9		13.5		2.7		6.0						
0.95 CI	31.6–54.8		8.7–45.8		6.7–27.2		0.8–10.3		3.2–11.4						

TABLE 3. Continued.

2. <5°N–12°S Dolphin spp.:	Spotted or spot. + spin.		Spinner alone		Common		Striped		Rough-toothed		All dolphins				
Flocks (F): Schools:	33 61		9 19		1 10		6 76		2 13		51 179				
Bird spp.	*n*	f	*n*	f	*n*	f	*n*	f	*n*	f	*n*	% *n*	f	*n*/f	% f/F
Sooty Tern	592	8	530	5			81	2			1,203	32.9	15	80.2	29.4
Noddy Tern															
Other terns	321[d]	3	20	2			8	1			349	9.6	6	58.2	11.8
RFB + booby[a]	1,743	13	10	2			8	1	13	2	1,774	48.6	18	98.6	35.3
Brown Booby															
Msk/Bf booby	5	1			30	1					35	1.0	2	17.5	3.9
Frigatebird	116	15	32	6			1	1			149	4.1	22	6.8	43.1
WTSW	7	3	19	2							26	0.7	5	5.2	9.8
Other shearwaters	10	1					1	1			11	0.3	2	5.5	3.9
WN/JF/DR petrels	8	4	28	2							36	1.0	6	6.0	11.8
Other pterodromas	3	2	16	2							19	0.5	4	4.8	7.8
Storm-petrels	28	4							10	1	38	1.0	5	7.6	9.8
Jaeger spp.	1	1	10	2							11	0.3	3	3.7	5.9
Gull spp.															
Tropicbird	1	1									1	0.0	1	1.0	2.0
Other			1	1			1	1			2	0.0	2	1.0	3.9
Total	2,835		665		30		100		23		3,654				
Mean flock size	16.3		35.9		30		8.0		4.7						
0.95 CI	7.8–33.7		25.5–48.6				1.4–47.0								

[a] Red-footed + Unidentified Booby; many of latter were probably RFB; Msk/Bf = Masked/Blue-footed booby; WTSW = Wedge-tailed Shearwater; WN/JF/DR Petrels = White-necked/Juan Fernandez/Dark-rumped petrels.
[b] Includes 100 *P. externa* from 1 flock in Central Pacific.
[c] Geometric mean of individual flock size.
[d] Includes unidentified terns, some likely being Sooty Terns.

TABLE 4. Number of birds (n) and mean flock size ($\bar{x}$) of species components of flocks according to three levels of total flock size. Flocks were associated with spotted and/or spinner dolphins.

Bird spp.	Total flock size							
	<50		50–150		>150		All	
	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$
1. 5°N–30°N								
Sooty Tern	217	6.78	468	22.29	347	31.55	1,032	16.12
Other terns	58	7.25	209	26.13	69	13.80	336	16.00
Booby spp.	459	9.00	1,312	37.49	5,366	178.87	7,137	61.53
Frigatebird	135	3.65	133	4.16	352	15.30	620	6.74
WN/JF/DR petrels	125	5.95	22	5.50			147	5.88
Other petrels	30	3.33	10	5.00			40	3.64
Wedge-tailed Shearwater	199	5.53	574	22.96	4,613	164.75	5,386	60.52
Other shearwaters	18	1.50	22	2.20	197	10.37	237	5.78
Jaeger spp.	151	5.21	280	11.20	1,766	60.90	2,197	26.47
Other	4	2.00			11	11.00	15	5.00
							17,147	
Mean no. spp./flock	3.45		5.32		5.87		4.45	
SD	1.56		1.92		1.70		2.02	
2. <5°N–12°S								
Sooty Tern	47	7.83	250	83.33	825	206.25	1,122	86.31
Other terns			10	10.00	331	82.75	341	68.20
Booby spp.	42	6.00	140	70.00	1,576	262.67	1,758	117.20
Frigatebird	28	2.55	20	5.00	100	16.67	148	7.05
WN/JF/DR petrels	8	2.00	8	8.00	20	20.00	36	6.00
Other petrels	31	6.00	16	8.00	1	1.00	48	6.00
Wedge-tailed Shearwater	26	5.20					26	5.20
Other shearwaters					10	10.00	10	10.00
Jaeger spp.			5	5.00	6	3.00	11	3.67
Other	1	1.00			1	1.00	2	1.00
							3,502	
Mean no. spp./flock	1.58		3.00		2.27		1.93	
SD	1.03		1.22		1.10		1.16	

NT waters. Only Sooty Terns were abundant in the flocks associated with this dolphin in ESTS waters (Table 3). However, frigatebirds occurred in six of nine flocks there.

There were few bird flocks associated with the remaining dolphin species. In those flocks, boobies, Wedge-tailed Shearwaters, frigatebirds, and Sooty Terns were often associated with the common dolphin, which frequently occurs near upwelling areas (Au and Perryman 1985). However, most numerous with this dolphin were the small, rapid-flying shearwaters, primarily Audubon's (*Puffinus lherminieri*) and Townsend's shearwaters (*P. auricularis*), which also seem attracted to upwelling and coastal areas. The few flocks associated with striped dolphins were notable in that none contained Wedge-tailed Shearwaters or jaegers. Flocks associated with rough-toothed dolphins did not include terns.

In ESTS waters flocks were less heterogeneous in species composition than in NT waters Whereas boobies, frigatebirds, Wedge-tailed Shearwaters, and jaegers all occurred in at least 50% of the flocks (i.e., >72 of 145 flocks) associated with spotted, spinner, and spotted plus spinner dolphin schools in NT waters, only frigatebirds occurred with such frequency (21 of 42 flocks) among these dolphins in ESTS waters (Table 3).

In these same flocks, the occurrence of Sooty Terns decreased from 44.1% in NT waters to 31.0% of the flocks in ESTS waters. However their numbers, as a percent of total birds in the flocks, rose from 6.0% in NT waters to 32.1% in ESTS waters. The overall mean flock size of Sooty Terns also increased greatly from 16.1 to 80.2 birds per flock in the ESTS waters (Table 3).

Although the percent occurrence of frigatebirds decreased in ESTS waters, it was never less than 50% of flocks among all spotted and/or spinner dolphin schools in either the northern or southern water type. Thus frigatebirds are good indicators of the presence of these dolphins (and also of yellowfin tuna), as fishermen well know, even though their average flock size was only six or seven individuals.

Finally, all individual avian species co-occurred most frequently with spotted and spotted plus spinner schools, as was shown above for flocks in general (Table 3). In 11 of the 16 different bird species or species groups from NT waters, 75% or more of their dolphin-associated flocks were associated with spotted or spotted plus spinner dolphins. In contrast, the percent of dolphin-associated flocks seen with schools of unmixed spinner schools was relatively low; among the different birds, the highest proportion of flocks with this dolphin was 25%, due to WN/JF/DR petrels. These observations all indicate that seabirds are primarily associated with the spotted dolphin, though the relationship is probably not direct.

BIRD-SPECIES ASSOCIATIONS IN FLOCKS

Because boobies, Wedge-tailed Shearwaters, jaegers, Sooty Terns, frigatebirds, and WN/JF/DR petrels were most prevalent in bird flocks, we looked at the possibility of interactions among these species. Initially, a comparison of the frequency distribution of flocks with 1, 2, . . ., *n* species with the distribution expected if the species had joined the flocks independently of each other (Pielou 1974) revealed significant nonindependence among the more abundant bird species in the flocks associated with spotted and spotted plus spinner schools and with common dolphin schools. We therefore looked for specific interactions among the above six principal species or species groups of birds in the flocks co-occurring with these two groups of dolphins, using Chi-square association tests. Significant species associations were found among the flocks co-occurring with spotted and spotted plus spinner dolphins, but not among flocks co-occurring with common dolphins, possibly because there were only 22 flocks with the common dolphin usable for such a test in our sample. The numbers of flocks with spotted and spinner dolphins in which various combinations of species pairs co-occurred are summarized in Table 5. The Chi-square tests were applied to these data, after rearrangement, and the results are also given in the table.

There were statistically significant, positive associations in these flocks from NT waters between boobies and frigatebirds, boobies and jaegers, boobies and Wedge-tailed Shearwaters, frigatebirds and Sooty Terns, and jaegers and Wedge-tailed Shearwaters. These positive associations suggest an interaction complex composed of boobies, Wedge-tailed Shearwaters, and jaegers, on the one hand, and a Sooty Tern-frigatebird interaction on the other, both linked by the booby-frigatebird association. Our observations indicate that the former complex is characteristic of dolphin-associated flocks from the eastern portion of NT waters, and the latter is characteristic of such flocks from the western and southern boundaries of the ETP.

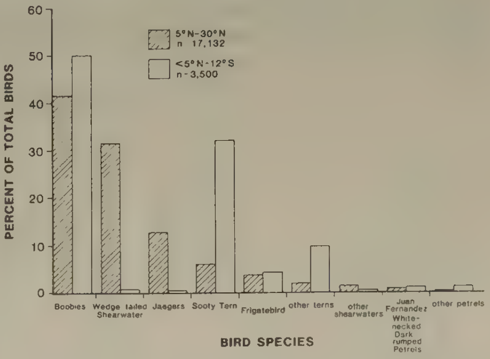

FIGURE 4. Percent of each bird species or species group in all flocks associated with spotted, spinner, and spotted-plus-spinner dolphin schools.

Significant negative associations were found between boobies and WN/JF/DR petrels in NT waters and between boobies and Sooty Terns in ESTS waters, where the latter were the only two abundant bird species in dolphin-associated flocks. The negative associations are probably best explained by geographic differences: in NT waters WN/JF/DR petrels occur primarily west of Clipperton Island (10.2°N, 109.3°W) where boobies are relatively uncommon and, when they do occur, are mainly the Masked Booby; in ESTS waters boobies are found near islands and continental coasts, while Sooty Tern flocks occur in the more oceanic habitats.

The significance of these associations should be viewed with some caution, because all possible combinations of these bird species were tested, a procedure that increased the chance for a Type 1 statistical error. If a "supercritical" level of significance were adopted to adjust for this possibility (Pielou 1974), only the Sooty Tern-frigatebird association would be significant. Nevertheless the correspondence of these associations with the species characteristics of dolphin-associated flocks from different areas and also the involvement of the sometimes kleptoparasitic frigatebirds and jaegers in the positive associations suggest real interactions. Furthermore, positive correlations between subflock sizes of certain species pairs can be demonstrated. Where pairs of species co-occurred in flocks over spotted and spotted plus spinner dolphins in NT waters, the Spearman rank correlation was significant ($P < 0.001$) and positive between the sizes of subflocks of Red-footed Boobies and Wedge-tailed Shearwaters ($r_s = 0.414$, $n = 65$), between Red-footed Boobies and jaegers ($r_s = 0.415$, $n = 66$), and between Wedge-tailed Shearwaters and jaegers ($r_s = 0.532$, $n = 59$). The correlation between subflocks of boobies

TABLE 5. Frequency of flocks (f) containing each bird species pair and the Chi-square association statistics from flocks with spotted + spinner dolphins.

Spp.		Co-occurring with:					
		Sooty	Booby	Frigate	WTSW	WN/JF/DR petrels	Jaeger
1. 5°N–30°N (131 flocks)							
Sooty Tern	f	57	50	48	40	10	37
	χ^2	—	0.35	10.05**	1.94	0.73	0.37
Booby spp.	f		111	81	74	8	74
	χ^2		—	4.93*	4.07*	−22.70**	8.10**
Frigatebird	f			90	59	9	60
	χ^2			—	0.71	−2.46	3.08
WTSW	f				82	9	59
	χ^2				—	−0.86	9.73*
WN/JF/DR petrels	f					18	9
	χ^2					—	−0.60
Jaegers	f						80
	χ^2						—
2. <5°N–12°S (33 flocks)							
Sooty Tern	f	8	0	2	1	2	1
	χ^2	—	−4.86*	−0.86	—	0.44	0.37
Booby spp.	f		13	6	0		
	χ^2		—	—	−0.71	−1.38	−0.05
Frigatebird	f			15	2	0	0
	χ^2			—	0.03	−1.99	—
WTSW	f				3	1	0
	χ^2				—	0.06	—
WN/JF/DR petrels	f					4	0
	χ^2					—	—
Jaegers	f						1
	χ^2						—

Note: χ^2 = Chi-square statistic of interaction table. df = 1. * and ** indicate $P < 0.05$ and <0.01 respectively. Examples of association test statistic for Sooty Tern and Boobies (5°N–30°N):

Both spp. occur together in 50 flocks.
Sooty Terns only occur in 57 − 50 = 7 flocks.
Boobies only occur in 111 − 50 = 61 flocks.
Neither spp. occur in 131 − 50 − 7 − 61 = 13 flocks.

A blank indicates χ^2 is very small or test is inappropriate; a minus sign indicates association is negative.

The value of χ^2 does not measure the magnitude of association, but can be converted to measure correlation in presence-absence data, equivalent to Yule's coefficient (Pielou, 1969:166).

and Sooty Terns was negative, but not significantly so.

DISCUSSION

Studies of seabirds can lead to insights into the ecology of pelagic communities, an idea perhaps best expounded by Murphy (1936). In the eastern tropical Pacific (ETP) the interactions of seabirds with dolphins and tuna reveal different species-specific behaviors and requirements for exploiting what must be sparse and patchily distributed prey. Tropical seabirds appear to have developed flight characteristics for efficient searching over large areas that have relatively light winds and for maneuvering rapidly over fleeting prey. Probably because prey is unpredictably concentrated and not abundant over large areas, pursuit diving by tropical seabirds has almost been eliminated (Ainley 1977); the birds feed near the surface instead. Many species show a strong tendency to form multispecies feeding flocks (Ainley and Boekelheide 1983) that are strongly dependent upon prey driven to the surface by predatory fish, mainly tuna (see Ashmole and Ashmole 1967).

THE RELATIONSHIP TO YELLOWFIN TUNA

We think that seabirds in bird-dolphin associations are primarily associated with the yellowfin tuna that co-occur with the dolphins, and that both birds and dolphins feed mainly on prey made available by the tuna. Yellowfin range primarily between the surface and the 20°C isotherm that typically lies in the upper thermocline (Blackburn 1965). Where the thermocline is shallow and its gradient strong, surface-feeding schools of medium to large tuna are often abundant (Sund et al. 1981). In contrast to most of the central and western Pacific, the thermocline depth in the ETP is frequently less than 30 m (Wyrtki 1964), and this seems to bring the yellowfin and their prey near the surface. Particularly in offshore waters of the ETP, these surface schools are composed of large yellowfin (Cole 1980) that feed and in-

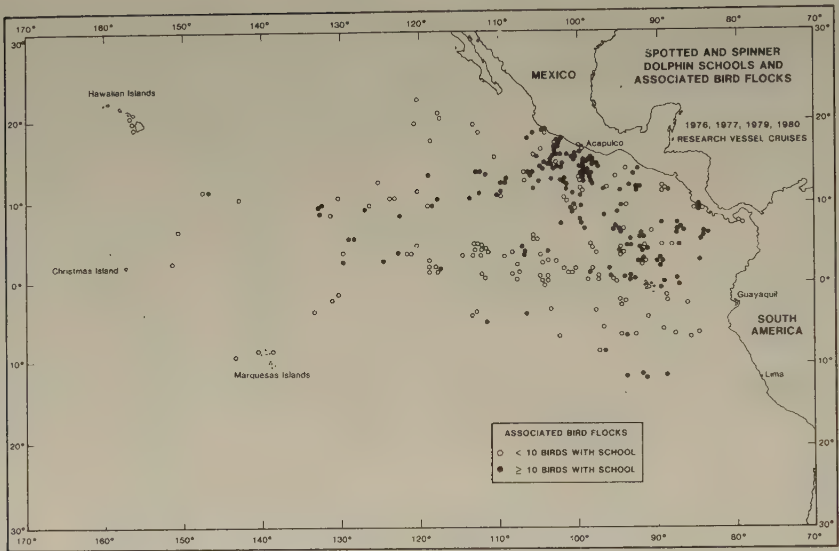

FIGURE 5. January–March distribution of spotted and/or spinner dolphin schools, with those schools accompanied by flocks indicated.

teract with dolphins and birds. It is only in the ETP that surface schools of yellowfin commonly occur (Cole 1980; R. Kearney, pers. comm.), and it is only there that birds are known to commonly co-occur with dolphins, and the dolphins with tuna, though all species involved in such associations are also found in the central and western Pacific.

Because seabirds in the ETP associate mainly with the spotted dolphin, the species primarily involved in the "tuna-porpoise" fishery for yellowfin, the birds appear to be ultimately linked to this fish. In this fishery, purse-seiners catch yellowfin by capturing (and later releasing) the dolphins that swim with this tuna (Perrin 1969). Although these tuna clearly follow the dolphins when the latter are chased by fishermen, we think such behavior is not typical of a feeding school (see below). Skipjack are also sometimes caught with the dolphins, but usually as a mixed catch with the yellowfin (Hammond 1981). Thus the areal pattern of bird flocks associated with spotted and/or spinner dolphins (Fig. 5) is essentially that of surface-schooling yellowfin (cf. Calkins 1975, Sund et al. 1981). Important fishing areas for this tuna extend westward along latitude 10°N from areas off Central America and southern Mexico; equatorial waters, where relatively few bird-associated dolphin schools occur, are not important in this fishery.

Both the yellowfin and the spotted dolphin are diurnally active species that probably feed together when associated (Perrin et al. 1973). Yellowfin are known to be diurnal feeders (Reintjes and King 1953, Cole 1980), and both spotted dolphins and these tuna frequently form large schools, especially on the ETP yellowfin fishing grounds (for these dolphins in northern tropical (NT) waters: $\bar{x} = 221.7$, $s = 217.2$, $n = 124$).

Seabirds co-occur less frequently with other species of dolphins (Fig. 2), and these other dolphins are correspondingly less often associated with yellowfin, consistent with our view that the birds follow the fish. Spinner dolphins in unmixed schools are relatively unproductive in tuna-porpoise fishing in comparison with spotted or mixed spotted plus spinner schools (Smith 1979, Hammond 1981), and spinner dolphins also rank third in degree of association with birds (Fig. 2). The spinner dolphin is also active diurnally and often forms large schools, but its food differs enough from spotted dolphins (Perrin et al. 1973) to indicate a less direct interaction with tuna. The common dolphin is much less productive for catching yellowfin in this same fishery, and birds correspondingly flock much less often with this species. The common dolphin also occurs in large, active schools but, unlike the spotted dolphin, it prefers habitats affected by upwelling (Au and Perryman 1985), and likely feeds at night (Evans 1971). The striped dolphin is a relatively large and diurnally active species, but it occurs in small schools ($\bar{x} = 60.8$, $s = 69.8$, $n = 187$) that are seldom seen with birds or fish (Au and Perryman 1985). It is seldom purposely caught by tuna fishermen. The few birds seen with this species were probably feeding on prey flushed unintentionally by the swimming dolphins rather than driven by associated tuna (this appears to happen with other dolphin species as well). The rough-toothed dolphin occurs in even smaller schools ($\bar{x} = 12.4$, $s = 9.9$, $n = 53$), and is a sluggish, inactive swimmer during the day (pers. obs.); it is only accidentally caught by purse-seiners. However this dolphin was more frequently associated with birds than was the striped dolphin. The reason may be that rough-toothed dolphins often occur near flotsam (pers. obs.), which attract fish, including tuna (Greenblatt 1979), and birds. This dolphin will feed upon small flotsam-associated fish (Pitman, pers. obs.; W. A. Walker, pers. comm.), but it probably does not associate directly with tuna.

The spatial arrangement of birds, dolphins, and tuna within feeding aggregations also suggests that the birds are primarily associated with the feeding tuna. It appeared from our shipboard observations that the birds worked mainly on the forward edge of the relatively scattered dolphin schools, sometimes among leaping tuna. Observations from helicopters provided better views: Au and Perryman (1982) saw feeding aggregations in which the bird flocks were often separated from the dolphins; R. P. Hewitt and G. L. Friedrichsen (unpubl.) described phalanx-like schools of tuna, attended by bird flocks, that swam at the front of the associated oval-shaped dolphin schools. These and the above observations suggest that birds and dolphins both take advantage of the feeding activities of tuna. It must be mentioned, however, that there are other interpretations; e.g., Norris et al. (1985) think it is the dolphins that are "nuclear."

THE RELATIONSHIP TO BIOLOGICAL PRODUCTIVITY

The development of seabird-dolphin-tuna associations appears to be promoted by increased biological production. It is significant that in the Pacific these associations are common only in the relatively rich ETP, especially within the "inner" areas (see fig. 75 in Wyrtki 1964) where the thermocline is especially shallow and where feeding situations are likely to develop close to the surface. These areas include the principal purse-seine fishing grounds, where in recent years (1972 to 1981) an average of 164,000 metric tons of yellowfin have been harvested annually (IATTC 1984), more than from any other surface fishery for this tuna. Because large schools of both spotted and spinner dolphins and surface-feeding yellowfin accompanied by birds occur in these waters, formation of opportunistic, multispecies feeding aggregations is to be expected (Evans 1982). Such feeding aggregations might start by convergence onto productive food patches by species adapted to finding and exploiting those patches. The aggregations may be long-lasting on the more productive patches, and interspecific competition there may be low (Schoener 1982). Commensal relationships may also develop, which may induce the species to stay together for some time.

Surprisingly, tuna are seldom associated with dolphins in the productive eastern tropical Atlantic (Levenetz et al. 1980; Stretta and Slepoukha, in press), where an important purse-seine fishery for yellowfin also exists. Fishing conditions there are similar in many respects to those in the eastern Pacific, including the frequent association of birds with tuna. The reason for this nonassociation is obscure. Is it because the dolphin fauna of the eastern Atlantic is different, or does it have to do with the abundance and structure of the prey population?

NATURE OF THE FEEDING INTERACTION

In the feeding aggregations observed in NT waters, prey driven to the surface, probably mainly by large yellowfin, is evidently abundant and diverse enough to allow dolphins and many bird species to feed at the same time. Differentiation of feeding behavior among the seabird species is quite apparent, although overlap in species or size of prey may be high (Diamond 1983). Boobies plunge-dive from above or snatch their prey from the air during aerial pursuit. Wedge-tailed Shearwaters feed on the water or, with the boobies, race at mid-height laterally along the front of advancing activity attempting to intercept unpredictably surfacing prey. Sooty Terns watch from vantages high overhead, then make swooping dives en masse wherever their component of prey surfaces. The second author has, on several occasions, observed groups of Sooty Terns ignoring the larger prey (especially flying fish) pursued by the other birds, then dropping to the surface seconds later to pick at smaller organisms. Evidently a wide spectrum of size, behavior, and perhaps species of prey is available, of which flying fish and juvenile ommastrephid squids are important both to the birds (Ashmole and Ashmole 1967, Diamond 1983, Harrison et al. 1983) and to the tuna and dolphins (Perrin et al. 1973). Prey driven to the surface may sometimes be superabundant. We have seen groups of apparently satiated boobies, Wedge-tailed Shearwaters, and jaegers resting on the water while others continued to feed. The associated dolphins meanwhile also appeared to be feeding. Small pods within the body of the school changed swimming direction often. Individuals could be seen "milling around," and what seemed to be diving behavior was observed. Sometimes both dolphin and tuna appeared to leap after the same fish or squid prey.

The positive associations found among the different species of birds is sufficiently explained by common attraction to these localized feeding situations, where food is made available by feeding tuna. The association of frigatebirds with boobies in NT waters and frigatebirds with Sooty Terns in equatorial/southern tropical/subtropical (ESTS) waters may be the most characteristic of the associations. Ainley and Boekelheide (1983) also found such associations in tropical seabird flocks, although their sample from the eastern Pacific was sparse, and dolphin-associated flocks were not treated specifically.

A DICHOTOMY IN THE PELAGIC COMMUNITY

Multispecies bird flocks associated with spotted and/or spinner dolphins and yellowfin tuna are characteristic of NT waters of the ETP. The contrast between these flocks and those dominated by Sooty Tern flocks without dolphins in ESTS waters is one of the striking biological features of the eastern Pacific. Boobies and frigatebirds are typical associated species in the multispecies flocks of NT waters, stemming from their similar, ready attraction to feeding tuna or tuna-dolphin schools. Boobies range far beyond their breeding colonies and are widespread with schools of surface yellowfin over the entire eastern Pacific fishing grounds. These colonies (mainly on Clipperton, Malpelo, Cocos, and the Galápagos islands) are probably the world's largest (Nelson 1978), an indication of the great advantage boobies gain from feeding with surface yellowfin.

Beyond the main fishing grounds for surface yellowfin, i.e., southwest of the Galápagos Islands and in the central Pacific, especially in ESTS waters, is a second community in which Sooty Terns predominate and associate with small fast-moving tuna that seldom co-occur with dolphins. The tuna are probably skipjack (Murphy and Ikehara 1955, Waldron 1964, Hida 1970), though small yellowfin and bigeye (*Thunnus obesus*) are sometimes seen, and frigate mackerel (*Auxis* sp.) may be involved. Dolphins, especially the spotted and spinner species, are much less abundant in these waters (Au and Perryman 1985) and evidently feed largely independently of tuna and birds there. Presumably, because large yellowfin there feed well below the surface, the link between dolphins and seabirds is broken.

As noted above, Sooty Tern flocks are notably abundant and characteristic of the region southwest of the Galápagos Islands and west of the Peru Current (Table 1; fig. 18 in Gould 1974; Pitman, unpubl.). (Although we have described Sooty Terns as being abundant in ESTS waters, they, as well as most other squid/fish-eating birds, are actually infrequent along the equator, at least east of about 130°W [Au et al. 1980].) Because there are only a few, relatively small, Sooty Tern colonies in the eastern Pacific (mainly on Clipperton and the Galápagos islands), most of the terns in this southeastern region must originate from the central Pacific, where large breeding colonies occur (see Table 1 in Gould 1974).

We have no information to the contrary regarding the qualitative features of the dichotomy discussed, although our samples during the northern summer were relatively sparse. In NT waters the tuna fishery "on porpoise" occurs year-round. This fishery expands far to the west of Clipperton Island during the summer, where Juan Fernandez Petrels predominate with tuna schools associated with dolphins. In ESTS waters, especially in the eastern Pacific, Sooty Terns may or may not be year-round residents, but they do not appear to be replaced by other birds from NT waters at any time.

SOOTY TERNS AND SMALL TUNA—THE FAR OFFSHORE LINK

Sooty Terns appear to be highly adapted for feeding with skipjack or skipjack-like tuna in less productive, far offshore waters beyond the surface yellowfin habitat, where they clearly dominate the avifauna. In contrast many other bird species of the eastern and central Pacific achieve their highest abundance in the more productive "inner" areas of the ETP, e.g., boobies, frigatebirds, Pomarine Jaeger, and light morph Wedge-tailed Shearwater (Pitman, pers. obs.). While this may result from greater interspecific competition faced by Sooty Terns closer toward shore (Diamond 1978), it is more likely a direct consequence of strong association with the tuna we think are skipjack (which occur throughout the tropical Pacific [Love 1971]). Just as boobies are widespread with surface yellowfin on the purse-seine fishing grounds, so too do Sooty Terns appear widespread with surface-schooling skipjack in far offshore waters. In the central Pacific small yellowfin are in surface schools close to islands, but skipjack schools predominate far offshore (Murphy and Shomura 1972). Since Sooty Terns also forage far from islands (Ashmole and Ashmole 1967, Diamond 1978, pers. obs.), this apparent avoidance of yellowfin habitat again indicates a strong proclivity to feed with skipjack. Admittedly these Sooty Terns may be associated with other small tunas, e.g., frigate mackerel, whose larvae have been found widely distributed in the southeastern Pacific (Love 1971); however adults of that species are caught primarily in coastal seas (Uchida 1981).

Sooty Terns seem to be near-obligate commensals with the small tuna they follow. They seem always to be either feeding with tuna schools or searching for such schools. Although occasionally reported to feed independently of tuna (Gould 1967, 1974), such feeding is rare, for Sooty Terns are unable to capture prey more than a few cm below the surface. This behavior is in contrast with most other birds that commonly feed with tuna. Only Sooty Terns seem to have achieved large success in exploiting that habitat where prey is made available largely by small tunas, and where prey independent of feeding tunas may be too infrequent for most birds. Still, the tuna-driven prey must be unsuitable or the energetic cost of following these tuna too high for most other birds; otherwise they would simply follow the Sooty Terns to feed. Sooty Terns cannot take large food (see Harrison et al. 1983), and this suggests that the prey made available to them is small. Nor can they rest long on the water (Gould 1974), as would be necessary if they were to feed heavily or on large prey, suggesting that the food patches are small and quickly dispersing. Sooty Tern adaptations for efficiently finding feeding tuna must include their continuous, agile flight, their high-flying habit that likely enables distant recognition of feeding behavior in other flocks or detection of surfacing fish (see Gould 1974), their strong flight for fast convergence on such feeding opportunities, and their seemingly constant vocalizations. The latter suggests cooperative foraging, perhaps expected in animals that exploit highly patchy and ephemeral prey (Horn 1968).

The Sooty Tern is evidently very successful in exploiting the far offshore habitat, being by far the most abundant bird in the southeastern and central tropical Pacific (Table 1; Gould 1974; Pitman, unpubl.). The small tuna are also very abundant (especially skipjack), and the two species seem to employ similar foraging tactics. As these far offshore waters are generally considered impoverished, the abundance of Sooty Terns there suggests very efficient foraging and also the possibility of underestimated biological production.

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6. Definition of Environmental Variability Affecting Biological Processes in Large Marine Ecosystems

ABSTRACT

Attempts to relate variations in reproductive success of fish populations to variability in the environment or in the biological community have been generally unsuccessful. A variety of processes, varying widely over a broad range of time and space scales, is potentially involved. Continuous observational coverage over such a range is impossible. Under the circumstances, defining the crucial variations involved presents a challenging set of problems. A serious need exists to develop generalizations that might provide the basis for unifying the available fragments of experience in a usefully coherent framework so as to make optimal use of the few empirical data available in a given situation. Interregional comparative studies, systematic observations of vertical distributions of organisms, studies of within-year variability in survival, and use of time/space statistical techniques, are advocated.

INTRODUCTION

In terrestrial ecosystems, the atmosphere has little capacity to store heat and other properties, and most sources of materials, etc., are fixed to a nonmoving substrate. In contrast, marine ecosystems exist in a continually moving, nonhomogeneous, dense fluid which has a large capacity to store heat, materials, and momentum. As a result, marine ecosystems are characterized by long period, large amplitude variability. During recent decades, catastrophic declines of some of the world's largest fishery stocks have had severe human consequences. During 1983 the ecosystems of the eastern Pacific were experiencing the most intense environmental anomalies of the past half century; it is likely that transient responses associated with this "El Niño" event will continue to perturb these ecosystems for years to come. The present lack of understanding of the mechanisms governing the interaction of environmental variation and fishery exploitation in causing large fluctuations in "recruitment" (i.e., the numbers of younger fish entering a fished population) is recognized as perhaps the most serious scientific problem hindering more effective management of living marine resources. Discussion in this chapter focuses on examples from eastern boundary current pelagic fishery stocks, as being illustrative of research problems common to a variety of large marine ecosystems and associated biological communities.

THE DILEMMA

Demonstrating that change occurs in these environmental/biological systems is not difficult. But to qualitatively and quantitatively specify the changes in a way that can form a basis for empirical understanding of the linkages involved presents a challenging suite of problems. Since the number of fish surviving to adulthood may be four orders of magnitude lower than the initial number of newly hatched larvae, such eventual survival is quite a rare event for individuals. Thus spot sampling of small numbers of realizations of individual life cycle events would be unlikely to yield useful information about total recruitment of a particular stock unit, even if the stock were homogeneously distributed and survival processes were linear. In fact, nonlinear interactions which are highly variable over a broad range of time and space scales typify the growth and mortality processes of pre-recruit fishes and most other marine organisms. Thus the ability to identify particularly crucial environmental conditions and to properly integrate their effects over the reproductive region and season associated with a stock unit, so as to reflect the net effect on reproductive success, appears to be a prerequisite for effective empirical approaches to understanding biological variability in large marine ecosystems.

Crucial Time Scales

Certain time scales appear to be of particular interest. For example, Lasker (1978) has indicated that anchovy larval survival may be seriously impaired by dispersion of fine-scale strata of microorganisms, required for food of "first-feeding" larvae, by wind-related turbulent mixing. Assuming that the time for accumulation of such concentrated strata is longer than one day, the relevant temporal considerations involve the interaction of the several days required for larval starvation, atmospheric storm activity with periods of variation of the order of a day to several weeks (examples shown in Figure 6.1), and the temporal variation of spawning activity over the spawning season.

At somewhat longer time scales (several weeks to several months) a variety of mechanisms may have significant effects. These include advection to favorable or unfavorable habitat, match/mismatch of spawning peak with food or predator organisms, interaction of temperature or food-regulated growth rates with size-dependent predation, adult feeding conditions which may affect formation of reproductive products.

The annual periodicity tends to be very dominant (Figure 6.1c); even in equatorial regions seasonal monsoon effects may be important. Biological processes tend to be well tuned to the annually repeating environmental variations, such that anomalies from normal climatic conditions are likely causes of disruptions in reproductive success of endemic populations. The dominance of the characteristic annual cycle of variation (compared to anomalies from it) causes problems in empirical analysis. For one thing, the degrees of freedom in within-year series available for empirical analysis tend to be substantially reduced because of the difficulties involved in properly filtering the large annual signal. Perhaps even more crucial is the fact that responses by natural selection to the large seasonal variation have probably, in many cases, resulted in seasonal tuning of basic biological--environmental linkages, such that underlying relationships among variables may be highly non-stationary over the annual cycle. These difficulties have motivated the conventional practice of studying recruitment processes on the basis of annual composites of the shorter scale events which may be actually involved.

On interyear time scales, marine biological time series very often exhibit substantial variance in the 3- to 12-yr period band (e.g., Figure 6.2). This is a band corresponding to appropriate periods of variation for various oceanic and atmospheric phenomena including baroclinic Rossby waves (Mysak et al., 1982) and variations of the global coupled ocean/atmosphere system known as El Niño-Southern Oscillation (ENSO) events. Other classes of variations also occupy this band (e.g., sunspots, etc.) and are sometimes incorporated into empirical "models" of biological variation; this is a band where the available time series is generally too short to contain more than a very few realizations of such multiyear variations and particularly in cases where direct linkage mechanisms are not well defined, the likelihood of spurious relationships is high.

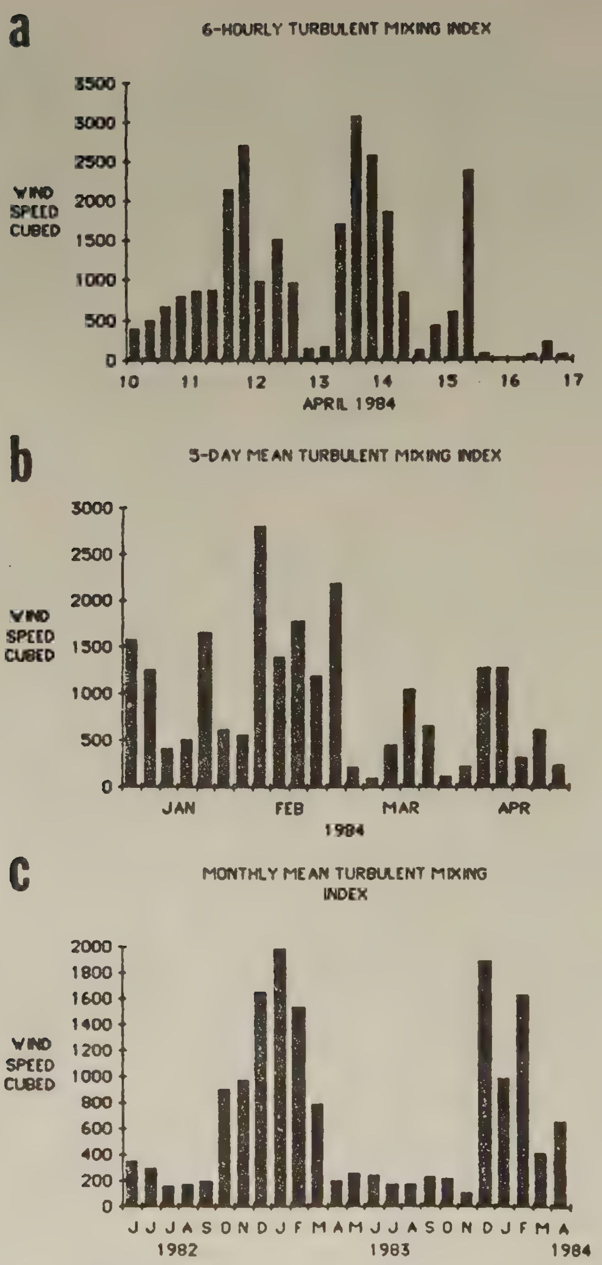

Figure 6.1. Index of rate of addition of turbulent mixing energy to the water column by the wind (e.g., Husby and Nelson, 1982). The index is computed as the third power (cube) of the speed of the large scale wind, as derived from synoptic surface pressure/wind analyses obtained from Fleet Numerical Oceanography Center. The location illustrated is off the coast of Washington State, at 48°N 125°W. Units are $m^3 sec^{-3}$. (a) 6-hourly synoptic computations. (b) 5-day means of 6-hourly computations. (c) Monthly means.

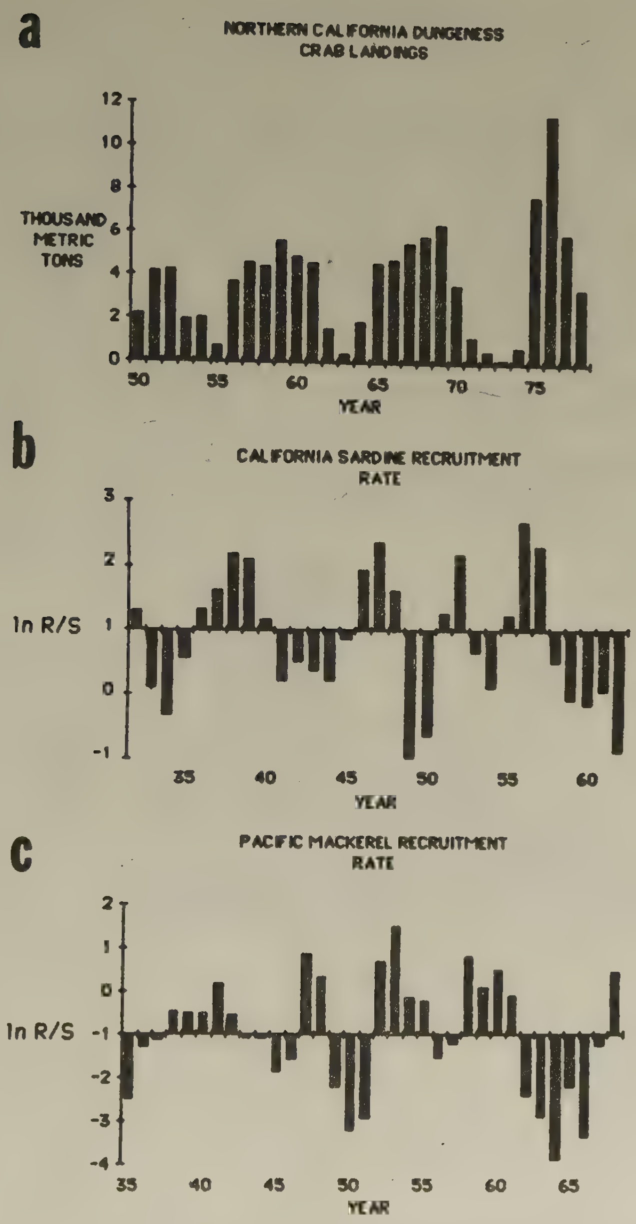

Figure 6.2. (a) Commercial fishery landings of dungeness crab in northern California (after Wild, 1983). Units are thousands of metric tons. Year indicated refers to the calendar year containing the end of a given annual fishing season. (b) Natural log of the ratio of California sardine recruits (10^6 fish) to parental biomass (10^3 metric tons). Values for 1947-1962 are based on the estimates of MacCall (1979). Values for 1932-1946 are based on the estimates of Murphy (1966). (c) Natural log of the ratio of Pacific mackerel recruit biomass to parental biomass (after Parrish and MacCall, 1978).

It is becoming apparent that there may be hierarchies of El Niño episodes, such that the events of 1957-1958 and 1982-1983 stand out as being global in character. These two episodes represent such extreme outliers in many California Current biological time series that they tend to control relationships based on "least square" fitting procedures. There is reason to believe that basic mechanisms underlying relationships among variables may be altered during these extreme episodes. Therefore, analysis of data from these particular years, together with data from the more normal years, may obscure any real relationships existing in either subset. The period between these two extreme episodes is 25 yr; this period is comparable to the total length of most pertinent data series from the California Current ecosystem. Deriving any substantial insight from an empirical analysis based on as little as two actual realizations is difficult, to say the least.

An even longer time scale may be highly pertinent to fishery management considerations. Smith (1978) has pointed out indications that the total biomass of pelagic fish stocks in the California Current system may have been as much as several times larger in the early part of this century than at the present time, or even than in the late 1930s when heavy exploitation commenced (Figure 6.3). This poses some important questions. Does the presence of large fish populations somehow increase the ability of the ecosystem to support the maintenance of these large populations? Do massive shifts in partitioning of basic organic production among exploitable and non-exploitable ecosystem components occur? Can management actions influence these shifts? Obviously, this is a time scale that we are not prepared to address experimentally and must rely on available "proxy" records, such as fish scale deposition rates (Soutar and Issacs, 1974) or guano deposits (e.g., Crawford et al., 1983), for empirical data analysis.

Crucial Space Scales

Lasker's hypothesis involves fine-scale vertical strata which may be centimeters or less in thickness. Crucial horizontal scales include spawning patch, food organism patch, juvenile school, small eddy, surface convergence zone, etc., diameters which may range from meters to kilometers (Smith, 1978; Owen, 1981). Offshore transport of reproductive products is thought to be an important regulator of reproductive success in eastern boundary systems (Parrish et al., 1983); pertinent offshore length scales are thought to include the internal Rossby radius of deformation (10-20 km off

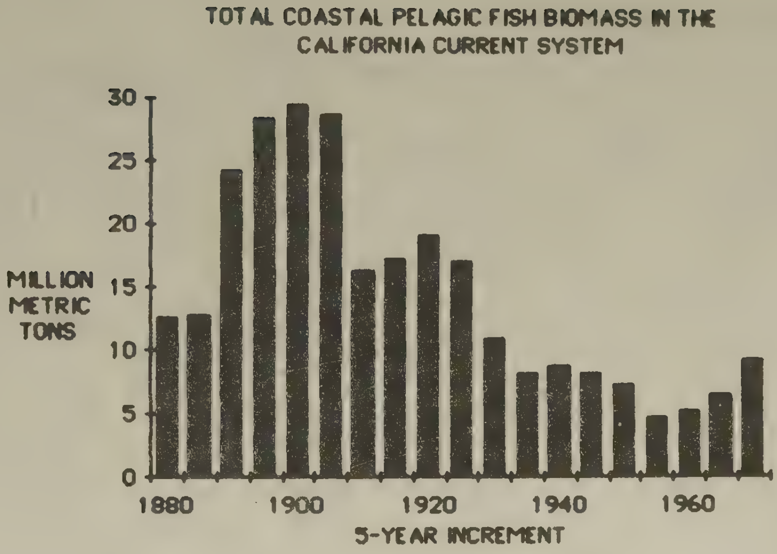

Figure 6.3. Biomass of the total coastal pelagic fish complex, consisting of sardine, anchovy, mackerel, saury and hake, in the California Current system at 5-yr increments, as inferred by Smith (1978) from analysis of present day stock sizes and from scale deposition rates determined by Soutar and Issacs (1974).

northern California, about four times greater in the anchoveta spawning region off northern Peru) and the width of the continental shelf (e.g., 20 km off n. California, 130 km off n. Peru). Major coastline features may delineate upwelling centers and coastal gyral circulations (length scales of tens to hundreds of kilometers). Spawning regions of coastal pelagic stocks may be of the order of a thousand kilometers in coast wise extent and several hundred kilometers in offshore extent. Larval drift and adult migrations may cover a thousand or more kilometers.

Environmental Data

Continuous observational coverage of such a range of time and space scales, using dedicated research ships, is not possible. One hope is to make use of routinely-gathered maritime weather reports which are available at 6-hourly synoptic intervals according to international convention. Historical files extend into the past century. Thus coverage is available over the range of desired time scales. However spatial resolution leaves much to be desired (Figure 6.4). Of some advantage is the fact that atmospheric length scales are large compared to oceanic length scales, and thus the major spatial scales of variation of wind, cloud cover (i.e., solar radiation input), etc., are at least minimally covered. Sea surface temperature varies relatively slowly compared to atmospheric properties and therefore observations from a number of synoptic samplings may be composited to improve coverage of finer-scale spatial features.

Fortunately, several currently-favored hypotheses concerning environmental regulation of reproductive success feature mechanisms involving wind, sea temperature, and solar radiation. In Lasker's (1978) hypothesis, wind-generated turbulent mixing energy is the causative factor. Wind-driven offshore surface transport, causing offshore loss of reproductive products (Parrish et al., 1983) is related to the product of the wind speed with its alongshore velocity component. On the other hand locally wind-induced coastal upwelling is driven by this same offshore surface transport which, therefore, may favor reproductive success at appropriate temporal and spatial lags by enhancing primary production and leading to adequate larval food particle concentrations, while being an unfavorable factor when coincident with spawning activity. Solar radiation also is involved in primary production, while sea temperature has direct effects on physiological rates; since larvae of many species inhabit the surface mixed layer, surface temperature often provides a useful indicator of

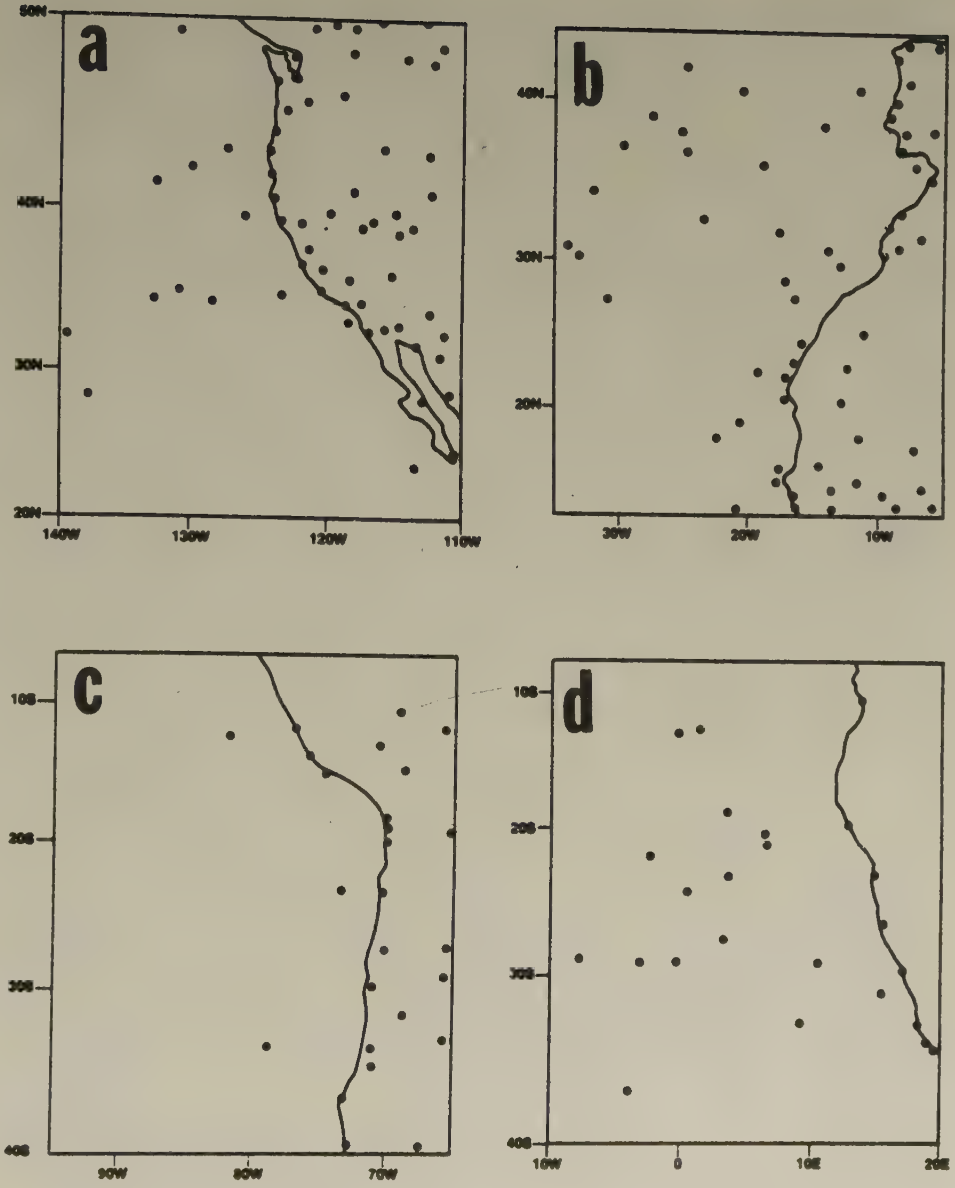
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Figure 6.4. Typical synoptic report distributions in the four major eastern ocean boundary upwelling regions (after Bakun and Parrish, 1980). (a) The California Current region (distribution shown is for 0600 GMT, 11 Jan 1980). (b) The Canary Current region (0000 GMT, 12 Feb 1980). (c) The Peru Current region (1800 GMT, 7 Feb 1980). (d) The Benguela Current region (1800 GMT, 7 Feb 1980).

temperature effects. Wind stress curl drives upwelling and downwelling seaward of the coastal boundary zone, controls convergence and divergence in the surface Ekman layer, and through Ekman pumping is a primary driving agent for variations in the baroclinic structure of the upper ocean (which may subsequently propagate westward as Rossby waves of interannual time scale).

Precision of estimates based on summaries of scattered maritime reports is a matter of concern. Since our focus is generally on interyear variability, difficulty in perfectly filtering the strong annual cycle exacerbates the low signal-to-noise ratio problem. Comparisons of random subsamples from a ten-degree latitude/longitude quandrangle adjacent to a typical temperate eastern boundary coast (Bakun, in preparation) indicate that only the more extreme interyear variations may be definable by simple areal summaries of reports at typical densities available. For example, it appears that at 200 observations per monthly sample we can expect that only about 20% of interyear differences (i.e., the difference between a monthly value and the value for the same month one calendar year earlier) of wind-mixing index (3rd power of wind speed) will be significant at the 0.1 level. For summaries of alongshore wind stress and cloud cover the situation appears to be somewhat better; about 60% of interyear differences in these properties appear to be significant at this level at a similar data density.

Additional information can be incorporated by means of objective analysis techniques (e.g., Holl and Mendenhall, 1972). These techniques spread information in time and space in a physically realistic manner, using dynamic or statistical models. Thus, observations from previous and subsequent synoptic samplings or from neighboring locations may contribute to a better estimate of the expected value at a gap in data coverage than possible from simple interpolation. Objective data analyses produced routinely by national meteorological agencies generally also incorporate elaborate error checking and quality control procedures based on degree of conformity of observations to physical reality as defined by the models. In addition large scale analysis of wind observations may be improved by the incorporation of barometric pressure data through the geostrophic coupling which is quite strong on large scales in extratropical regions. Thus, the physical mechanisms underlying the models, and the temporally and spatially adjacent data, constitute additional information which may improve the estimates. Thus, we may expect that significance of indicated interyear differences in monthly values computed from objectively analyzed fields (e.g., wind mixing index as shown in Figure 6.1c) may be improved relative to simple areal averages of reports. However, the complexity of the analysis procedures make it difficult to quantify the expected degree of improvement.

Monthly "coastal upwelling indices" based on analyses of wind and atmospheric pressure, are intended to indicate interyear variations in wind-induced offshore transport of surface waters and resulting coastal upwelling. They have been found to yield significant correlations with a wide range of types of biological variations in the California Current region (Bakun and Parrish, 1980), involving such fishery species as Pacific sardine, northern anchovy, Pacific mackerel, dungeness crab, English sole, coho salmon, bonito, hake, and shrimp. However, precision estimates for the indicated variations are not available and associated difficulties in assigning confidence estimates on the apparent relationships limit their utility.

Specifying shorter-scale variations, in the energetic "storm event" frequency band (e.g., Figures 6.1b and 6.1c), is less of a problem due to the large amplitude of the signal relative to the noise (almost any sort of analysis of reports is adequate to indicate presence or absence of storm conditions). However, specification of the affected biological characteristics is seldom available on corresponding scales, and so the tendency has been to search for "bulk" relationships which integrate larger (but unfortunately lower in amplitude) scales of variation.

Measurements at coastal installations offer useful sources of data, covering desirable ranges of time scales at consistent geographic locations. Spatial aspects are less satisfactory. Coastal sea temperature measurements may sample very local scales of variation. Wind measurements are often distorted by coastal topography. Sea level measurements do reflect rather large scales but these scales are difficult to specify, which is a large problem because the main effect of sea level on the processes of interest is through its gradient.

Statistical Significance

In summary, we face a problem of substantial complexity with very little empirical information covering the range of time and space scales determining the final level of recruitment to a total stock. As long as we must attempt to relate "bulk" effects on larger scales (with lower signal amplitudes) than those on which the crucial processes are acting, we must expect weak relationships which do not have a high degree of statistical significance given the limited degrees of freedom available on interyear scales in fishery and other biological time series. In most types of situations it would be almost inconceivable that any one environmental mechanism could so consistently dominate survival processes as to yield a strong univariate relationship that was not, to some degree, spurious. This is not to say that a well-formulated exploratory data analysis is not a useful activity, or that its results should not be reported. But mere searches for relationships meeting significance criteria (i.e., publishable), among various combinations of data sets and formulations, are not very enlightening. The question of how to make use of the weak relationships, which may represent realistic levels of control by particular mechanistic linkages, poses a major challenge.

SOLUTIONS

An obvious need is to develop generalizations that might apply to wider classes of fisheries or ecosystems, and thereby provide a basis for unifying the available fragments of experience in a usefully coherent framework. Certainly, if each separate situation is fundamentally different from all others, there does not seem to be much hope of developing substantial understanding of any. For that matter, there would probably be few situations worth intense research effort if expected results were to have no broader sphere of application. The following paragraphs present some suggestions as to approaches which might lead to progress in resolving some of the problems outlined above.

Interregional Comparative Studies

The large marine ecosystems of the four major subtropical eastern ocean boundary regions appear to be controlled by similar environmental dynamics and contain very similar assemblages of exploitable pelagic fishes (Table 6.1). They also exhibit similar histories of fishery growth and abrupt decline (Figure 6.5). The similarities suggest that the fish communities in these different systems may function somewhat similarly with respect to their environments and may have reproductive strategies adapted to solving similar environmental problems. Since natural selection implies that reproductive strategies reflect responses to the most crucial factors regulating reproductive success, compelling patterns of correspondence among reproductive habits and environmental characteristics are likely to reflect important causal mechanisms.

For example, Parrish et al., (1983) examined characteristic seasonal distributions of temperature,

TABLE 6.1.

Dominant anchovy, pilchard, horse mackerel, hake, mackerel, and bonito in the four major eastern boundary currents (after Bakun and Parrish, 1980).

California Current	Peru Current	Canary Current	Benguela Current
Engraulis mordax	*Engraulis ringens*	*Engraulis encrasicholus*	*Engraulis capensis*
Sardinops sagax	*Sardinops sagax*	*Sardinia pilchardus*	*Sardinops ocellatus*
Trachurus symmetricus	*Trachurus symmetricus*	*Trachurus trachurus*	*Trachurus trachurus*
Merluccius productus	*Merluccius gayi*	*Merluccius merluccius*	*Merluccius capensis*
Scomber japonicus	*Scomber japonicus*	*Scomber japonicus*	*Scomber japonicus*
Sarda chiliensis	*Sarda chiliensis*	*Sarda sarda*	*Sarda sarda*

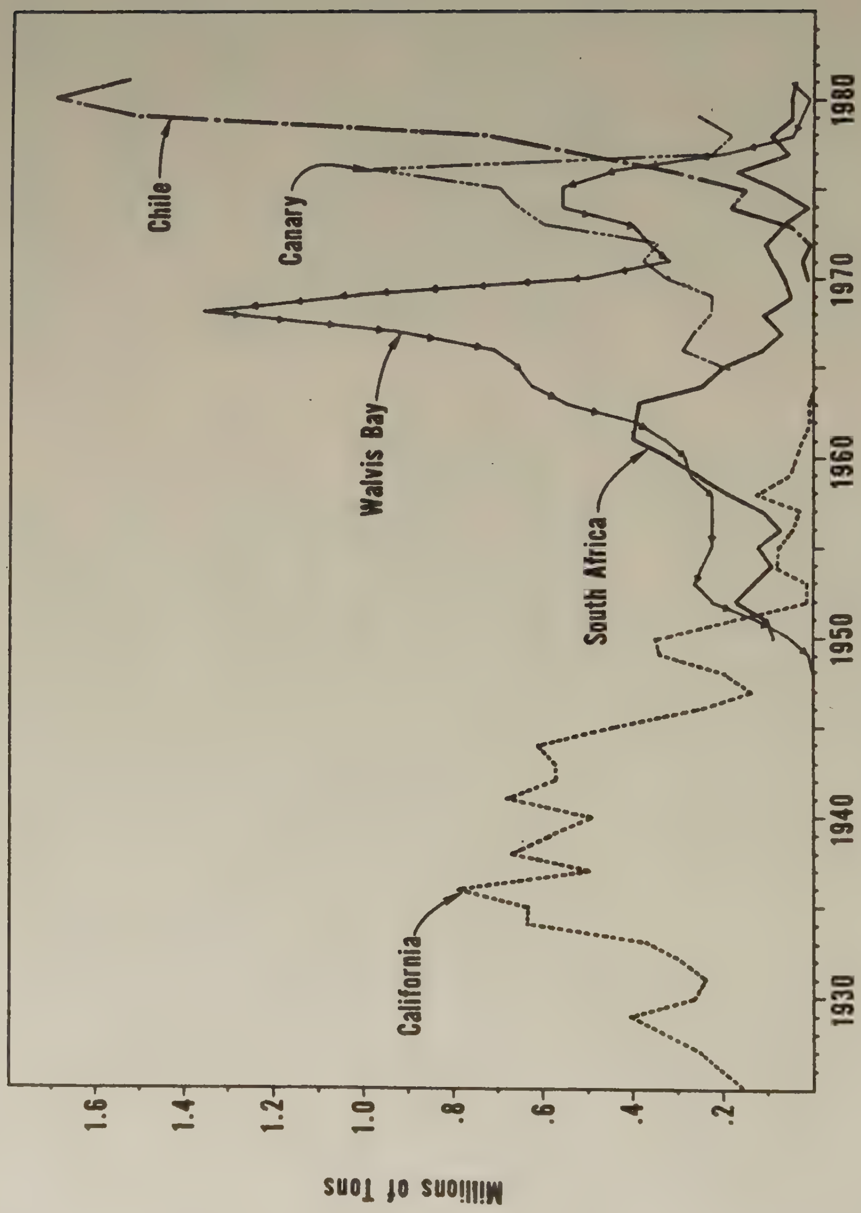

Figure 6.5. Annual sardine landings from several eastern boundary current stocks (after Parrish et al., 1983). Walvis Bay and South Africa refer to the two major Benguela Current stocks.

surface drift, wind mixing energy input, and upper water column stability in the California, Peru, Canary, and Benguela Current systems. They found several interesting patterns with respect to available information on spawning of anchovies and sardines. Avoidance both of substantial wind mixing of the upper ocean layer and of strong offshore transport seemed to be dominant characteristics of spawning habitat selection. Selection for any particular optimum temperature, within physiological limits, seemed less important. These findings, which are independent of time-series results, provide a guide for selection of variables for time-series modelling in a way that makes improved use of the scarce degrees of freedom available.

Certain initially-puzzling discrepancies from general patterns have proven enlightening. For example, it was noted that the spawning peak of the Peruvian anchoveta occurred in austral winter, the season of strongest offshore surface transport, rather than at the season of weakest transport, as is the general case. However, when viewed in conjunction with mixed layer depth climatology the discrepancy appears to be resolved; seasonal variation of mixed layer depth off Peru proceeds in phase with that of transport but has greater amplitude, with the result that the thinner mixed layer of austral summer is apparently carried offshore nearly four times as fast as is the deeper winter mixed layer, even though the winter volume of transport is nearly twice as large. Thus spawning indeed appears tuned to minimize the rapidity of offshore loss of eggs and larvae. This resolution of an initial discrepancy points out that, in treating the mechanism of offshore loss of reproductive products which are distributed through the mixed layer, wind-driven surface (Ekman) transport should ideally be divided by mixed layer depth to yield an Ekman velocity of the mixed layer. In this way, two environmental variables are combined to yield a single more meaningful variable, thereby preserving degrees of freedom for fitting additional pertinent variables in empirical modelling efforts.

Beyond comparisons of spawning habitat climatology, it would seem to be fruitful to compare actual time-series relationships among similar regional ecosystems. Under an assumption of analogy, weak empirical relationships having a similar general form in several systems could be assigned greater confidence than would otherwise be warranted. Conversely, a high correlation found in one system might be questioned if no suggestion of a similar type of linkage was found in other systems appearing in other respects to be analogous. Arraying identically formulated empirical models from different regional systems might yield patterns among model parameters that could provide new insights as to proper transfer of experience among systems in order to predict outcomes of actions taken in one system from the record of similar actions taken previously in other systems. Such efforts would ideally involve interregional and international cooperative activities to assemble analogous variable sets, and provide informed interpretation.

Observational Activities Aiding Scale Integration

Comparative studies are an example of a deductive (i.e., indirect) approach. Because of the great range of crucial scales, more direct experimental approaches tend to involve an impractical observational investment. However, it may be possible to save some effort by designing sampling schemes that would enhance our interpretation of larger scale, more easily specified variations in terms of their effects on processes occurring at smaller scales. As an example, it is conceivable that weakly swimming organisms might exert considerable control over their advection by simply adjusting their depth in the water column. In subtropical eastern ocean boundary regions, clear weather often accompanies an offshore atmospheric high pressure system which produces equatorward winds and corresponding offshore-directed surface Ekman transport. Stormy weather would involve the opposite conditions leading to onshore surface transport. Thus, organisms that position themselves deeper in the water column during clear weather than under cloudy conditions would be aided in avoiding detrimental offshore advection. In addition, the very surface "skin" of the ocean travels in a different direction with respect to the wind than does the Ekman layer; other surface skin effects may act somewhat independently of the wind, e.g., onshore movement of surface slicks generated by passage of internal waves (Shanks, 1983). Knowledge that has been developed concerning the physical transport mechanisms would allow interpretation of vertical biological structure in terms of the function and importance of these mechanisms in natural selection. It appears that well-determined characteristic vertical distributions of planktonic organisms are not widely available, although the sampling techniques are not extraordinarily difficult (e.g., compared to quantitative population estimation). Some detailed sampling of the vertical distributions under different conditions, which might constitute a practical degree of effort, could reveal much about the manner of biological response to these conditions. With increased understanding of these responses, monitoring of the larger scale conditions might in some way substitute for continuous time/space observation of the actual fluxes of organisms.

Sampling of "Integrated" Effects at "High Signal" Scales

The logical way to seek the greatest empirical return for an observational investment is to sample the integrated results of processes occurring on smaller scales, at scales which are more readily sampled but where the signal-to-noise ratio remains relatively high. Conventional recruitment estimates derived from fishery statistics integrate within-year variations to yield a single annual composite. This process suppresses and obscures signals from shorter scale, possibly higher amplitude, components of the variability in survival. In addition, the process of forming composites necessitates an integration of energetic environmental "event" frequencies with accompanying decline in signal-to-noise ratio in specifying the environmental context. Working with annual composites also yields minimal degrees of freedom for empirical investigation of linkages.

In connection with the International Recruitment Project (IREP) of the Intergovernmental Oceanographic Commission's Program of Ocean Science in relation to Living Resources (OSLR), an experimental program has been conceived (Anon., 1983) which appears to be uniquely promising because it addresses the energetic within-year scales. It involves determining fish egg or larval abundance within a spawning region of a given stock unit, at increments through an extended spawning season. Subsequent survival is estimated by sampling late larvae or early juveniles, determining their birthdate distributions using recently-developed daily ageing techniques (Methot and Kramer, 1979), and comparing birthdate distributions to the corresponding estimates of egg abundance. Interference from annually-tuned mechanisms is minimized by the process of incrementally-determining both the inputs (eggs or early larvae) and the outputs (survival). Integrations of environmental conditions over the intervening time increments can then be examined to determine the degree of "fit" represented by alternate causal mechanisms and formulations. The program does imply a considerable sampling effort to adequately encompass the pertinent scales of variation over a total stock unit.

Time/Space Statistical Analysis

With the rapid increase in economical computing power, application of a very powerful class of methods of exploratory data analysis is finding increased application in fishery/environment studies. Basically, they allow the computer to do much of the work in sorting out time/space structures among data sets (work that may previously have been done less systematically by laboriously plotting and comparing time series of mapped distributions). For example, Mendelssohn and Roy (in press) have used *spectral empirical orthogonal functions* to demonstrate wavelike propagation in tuna distributions and in sea temperature which conforms to a Kelvin wave interpretation. Such examinations of space/time structures in the behavior of ecosystem components, in the light of known structures in the characteristics of particular environmental mechanisms, appear to offer substantial promise. However, it may be well to note that rather than being a mechanical process, both the formulation of the variables and the application of the methods involve important interpretive aspects requiring skill and judgment; without these, the increasing ease of access to electronic data banks, substantial computing power, and software for complex analysis procedures, would appear to have potential for generation of a much greater volume of published output, without any correspondingly greater degree of enlightenment, than the correlation searches of the past.

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LOCAL RETENTION OF PLANKTONIC EARLY LIFE STAGES IN TROPICAL REEF BANK DEMERSAL SYSTEMS: THE ROLE OF VERTICALLY-STRUCTURED HYDRODYNAMIC PROCESSES

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ABSTRACT: The question of the extent to which local tropical reef bank demersal fish populations may constitute open or closed systems with respect to recruitment is crucial to resource management as well as to scientific investigation of the causes of recruitment variability. Connotations of the almost universal commitment to extended periods of pelagic larval drift among coral reef fishes, as well as certain evidence of largely locally-based recruitment in these systems, are discussed. A variety of vertically-structured hydrodynamic processes, pertinent to the problem, are introduced. An observational focus on vertical structure in both biological and physical aspects is advocated as offering a means to circumvent extreme difficulties involved in applying conventional recruitment research methodologies to tropical systems. Interregional comparative studies may offer a particularly efficient avenue of inquiry. Important inputs from a broad range of marine scientific specialities are envisaged.

1. INTRODUCTION

The early life stages of fish species inhabiting oceanic reefs and banks are characterized by extended periods of planktonic drift, during which the mean ocean surface currents would tend to carry freely drifting offspring great distances from the local spawning habitats of their parents. This has led quite naturally to a perception of the effect of local spawning as being mainly a contribution to some larger regional-scale (or even ocean basin-scale) 'pool' of dispersing larvae from which recruitment to the various local populations occurs by random diffusion, or by direct advection by prevailing currents from upstream populations. This perception lends support to a view that fishery management on a local scale may be futile, or at least nonessential and locally unprofitable. However, various fragments of evidence that this may not always be the case are discussed below. It is arguable that this question of the spatial scale from which recruitment is ordinarily generated is in fact the most crucial aspect of the recruitment problem with respect to immediate utility of scientific results in improving management of human impacts on tropical oceanic demersal resources.

Recent studies in which coherent observational programs have been maintained over interyear time scales (e.g., Williams,1980 & this vol.; Victor,1983; Doherty, 1983) have suggested that even unexploited coral reef fish populations may not generally be in resource-limited or predation-controlled equilibrium, but rather that their population dynamics may be controlled principally, as in other types of studied fish stocks, by recruitment variability. In addition, synthesis of information obtained from artisinal fishermen as well as from scientific studies (Johannes,1978,1981), and computer simulations incorporating vertical migratory behavior (Doherty et al.,1985), have provided new hypotheses as to the role of larval drift in reproductive stategies of fishes associated with coral reef systems. The capacity of vertical migratory behavior to interact with vertical structure in the flow field to produce larval trajectories differing greatly from ambient flow patterns has been strikingly demonstrated with respect to prawn stocks of the Gulf of Carpenteria (Rothlisberg,1982; Rothlisberg et al.,1983).

2. WHY PELAGIC STAGES ?

The fact that marine organisms associated with oceanic islands and banks face a problem of conserving, rather than dispersing, their pelagic stages has been recognized for many years. Boden (1952) suggested that planktonic forms were maintained in the vicinity of Bermuda by convergences associated with an observed anticyclonic circulation pattern over the subsurface bank underlying the island group. Ehrlich (1975) cited evidence that species inhabiting the isolated oceanic island, Johnston Atoll, were not recruited from the Hawaiian Islands, the nearest upstream source, but had characteristics indicating endemic reproduction; this led him to remark on the "enormous losses" of reproductive products which must be borne by the local marine fauna. Johannes (1978) enumerates various adult reproductive behaviors apparently explicitly adapted to cause the reproductive products to be transported offshore where they would be most subject to such losses. Sale (1980) commented on the ubiquity of the pelagic reproductive mode, and noted that in only a single case has absence of a pelagic phase in the early life history of a coral reef fish been demonstrated. A typical length for the pelagic phase appears to be of the order of three to ten weeks (Brothers et al.,1983; Victor,1986).

It is possible that very large lagoons such as that of Enewetok Atoll, which appears to have a mean water residence time of the order of a month (Atkinson, Smith & Stroup,1981), could be important to local larval retention. However, reef lagoons of more common sizes appear to have such short flushing times (Leis,1982; Wolanski & Picard,1983) that retention of significant numbers of larvae through their entire pelegic phase is unlikely (Williams et al.,1984). Thus it seems improbable that retention of reproductive products in enclosed lagoons can be a primary basis for widespread reproductive adaptations.

This leads to an obvious question: Why does the pelagic mode of reproduction so dominate among fishes of these systems? This can be re-phrased: How have the fishes utilizing the pelagic mode of reproduction been able to compensate for the apparent overwhelming reproductive energy losses, so as to avoid having been replaced by fishes having more conservative evolutionary adaptations such as livebearing, continuous brooding of offspring, etc.? If we believe in evolution by natural selection, we must conclude that the prevalence of the pelagic mode is due to the fact that it has turned out to be more successful, on the long term at least, than any of the alternatives that could be developed.

Doherty, et al. (1985) cite Barlow's (1981) suggestion that dispersal is necessary to prevent extinctions in a situation where an uncertain environment cannot ensure maintenance of viable local populations of spawning adults. Few are likely to argue with that line of reasoning (although, if this were the sole function of the pelagic reproductive strategy, one might wonder if the particular need might not be more efficiently met by other adaptations such as intermittent migrations of 'pioneer' groups of adults). Doherty et al. (1985), while accepting Barlow's general statement, remain unconvinced that it accounts for the extreme degree of dispersal that actually occurs. They specifically "do not address the question of why these animals 'broadcast' rather than 'brood'" but suggest that species committed to pelagic offspring will be under selection to disperse siblings to spread the risk of failure among members of a cohort. They support this hypothesis with a computer simulation wherein larvae which were dispersed in an environment containing a horizontally patchy food distribution, and possessed vertical migrating behavior by which their position relative to the surface flow pattern could be altered when the relation to food distribution was unfavorable, experienced better average survival than larvae which did not disperse. Johannes (1978) notes the disadvantages of live-bearing, including low fecundity, increased stress, and increased vulnerability of adults carrying young; his major point is that given the egg-laying reproductive mode, the pelagic strategy functions to remove eggs and hatched larvae from the intense predation of the reef areas inhabited by the adults.

2.1 An 'aside': Is there a potential long-term advantage of erratic recruitment?

In this section we turn briefly to a speculative discussion of another factor possibly favoring the prevalence of the pelagic reproductive mode among the fishes successfully inhabiting these systems. (Note that the degree of 'real-world correctness' of the particular line of reasoning presented in this section is not deemed to be in any way crucial to the main line of argument developed in subsequent sections of the paper; it is inserted here because the ideas are related to the other topics being developed and also might constitute some useful hypothetical framework for interpreting results of potential interregional comparative studies which are advocated later in the paper.)

Intermittency, characterized by peaks of high abundance separated by very much wider intervals of very low abundace, is quite a pervasive characteristic of marine populations. Intermittency in time and space may serve, among other possibilities, to defeat predator populations by denying them a continuously accessible food source. Since a predator can have only a limited energy storage capacity, presenting it with much more food than can be utilized at each encounter, while stringently minimizing the frequency of encounters, favors maintenance of the prey population's biomass. Perhaps more importantly, such a tactic prevents growth and maintenance of large resident predator populations which could decimate, or even cause extinction of, the prey population. Schooling behavior is one way spatial intermittency is achieved. In the case of reef/bank demersal systems, space may be too valuable a resource to expend in this manner. Therefore, temporal intermittency may offer the only means by which the growth of destructive levels of predation pressure might be interrupted.

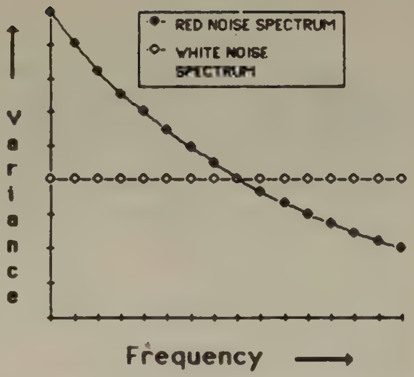

Figure 1. Example 'red noise' and 'white noise' spectra.

A temporal analogue of schooling behavior consists of intermittent pulses in abundance. Shorter term intermittency allows a predator population to be temporarily overwhelmed by numbers of prey such that adequate survivors may pass through a particularly vulnerable stage (e.g., transition to demersal life style, etc.) to recruit to the adult stock. Longer term intermittency may serve to preclude the establishment of a dependent predator population. In fact, some non-regular mixture of frequencies (i.e., unpredictable and therefore impossible for a predator to counter by any selective adaptations) may be an optimal situation for a population which is seriously vulnerable to predation. A "red noise" spectrum of variability (i.e., increased variance at lower frequencies, in contrast to "white noise" which has equal variance across the spectrum (Figure 1)), where groups of episodes of extremely low prey availability are embedded within longer periods of relative scarcity, could be particularly advantageous in causing collapse of specialized predator populations.

Development of biological adaptations to achieve such intermittency in abundance may not be feasible. For example, a survival advantage to more adapted individuals over less adapted individuals in the population, which could thereby direct the selection process, would not exist in this case. Also, synchronization of irregular variability (as opposed to regular periodicities) among individuals, so that it could be effective in this sense, may be difficult via purely biological mechanisms. However, variability in nearly all aspects of the earth's coupled ocean/atmosphere hydrodynamic system is known to be characterized by red-noise spectra. Organisms whose abundance at particularly vulnerable stages (e.g., at recruitment) is subject to this variability may be favored over those with more uniform reproductive output. One mechanism by which demersal organisms might not only incorporate the ocean's available red-noise variability via pelagic early life stages, but also experience reduced losses of those stages from the local habitat and thereby achieve large episodic recruitment pulses, is described in the following section. (Note that this argument does not necessarily depend on existence of any need to defeat directed predation on recruits on the shorter-term year-to-year time scale; the fact that no directed predator on these stages may be present in substantial abundance could be a result of the fact that intermittency has precluded its establishment. To the question of "why would the adults not need similar intermittency in abundance?", a partial answer may lie in the array of individual reef structures themselves, as constituting a spatial intermittency constraint with respect to organisms of large enough size to be major predators on adult reef fishes.)

3. THE STRATIFIED TAYLOR COLUMN

A classical laboratory demonstration (Taylor,1923) of the special properties of fluid flow in a rotating coordinate system (note that for large scale flows such as ocean currents, the earth functions as a rotating system) proceeds as follows. A large flat-bottomed tank of water is set on a rotating turntable. Some solid object is placed on the tank-bottom so as to represent a 'bump' protruding from the tank floor. A dye marker is placed in the water above the bump. If the object is then moved slowly along the tank floor, the dye in the water above is observed to follow along with it, showing that the water column above the bump is effectively trapped relative to the bump.

The same phenomenon occurs if the bump is stationary and the water is moving relative to it (analogous to a submerged bank in the path of an ocean current). The

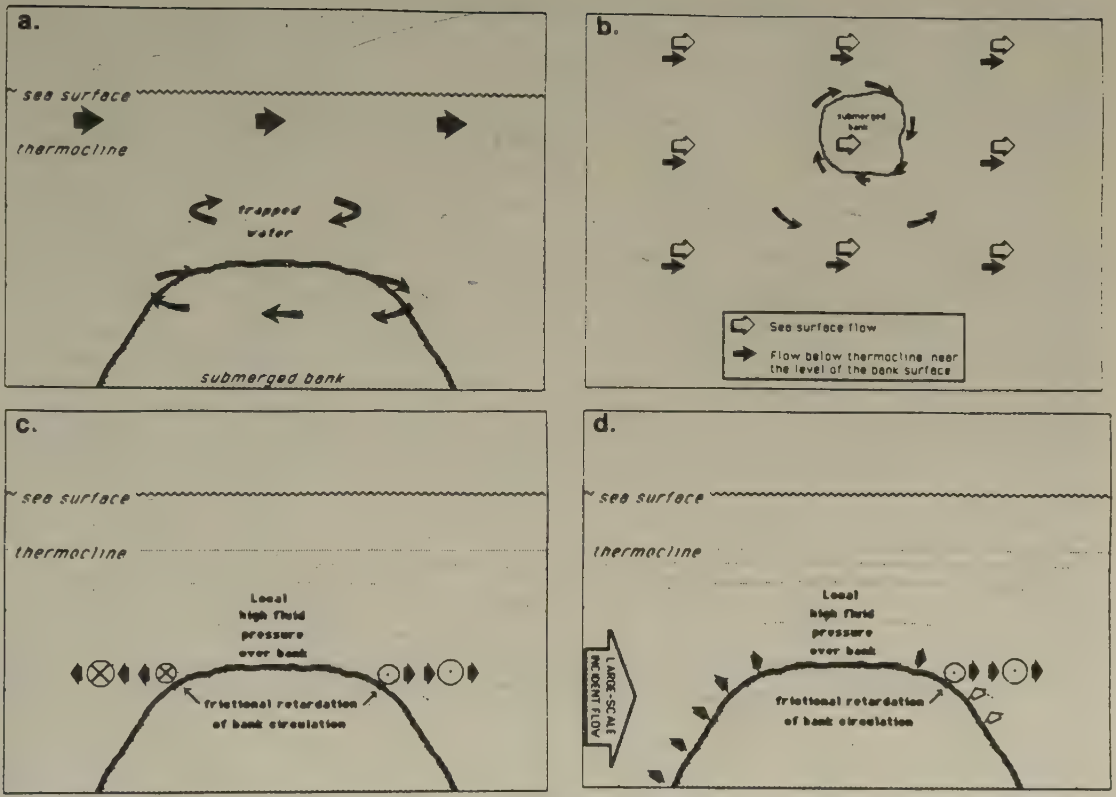
a.
sea surface
thermocline
trapped water
submerged bank
b.
submerged bank
Sea surface flow
Flow below thermocline near the level of the bank surface
c.
sea surface
thermocline
Local high fluid pressure over bank
frictional retardation of bank circulation
d.
sea surface
thermocline
LARGE-SCALE INCIDENT FLOW
Local high fluid pressure over bank
frictional retardation of bank circulation

Figure 2. Schematic representation of a stratified Taylor column over a submerged bank: (a) horizontal view; (b) plan view; (c) profile view indicating frictional retardation of flow adjacent to bank surface resulting in sub-geostrophic flow and associated unbalanced pressure gradient, leading to a secondary radially-directed outflow (short black arrows) from the bank area (circles containing 'x' indicate flow of the primary around-bank circulation into the plane of the figure; circles containing dots indicate flow out of the figure); (d) representation of upwelling circulation which may balance radial outflow (see text). Note that these two-dimensional representations are heuristic rather than exact; in the real situation, interaction with the pressure gradient which is in balance with the large-scale incident flow causes the situation to be inherently three-dimensional. Examples depicting more complex actual numerical model results are presented by Huppert & Bryan (1976).

the scientists who originally deduced the effect theoretically (Proudman,1916; Taylor,1917). Interestingly, the Great Red Spot of Jupiter has been attributed to the existence of an enormous Taylor column in the Jovian atmosphere (Hide,1961). Shomura & Barkley (1980) suggested Taylor columns as an explanation for the ability of populations of organisms having pelagic egg and larval stages to maintain themselves as components of ecosystems associated with banks and seamounts.

Hogg (1980) provides a useful review of recent application of Taylor column theory to the circulation of a stratified ocean. In the stratified case the Taylor column effect is bottom-intensified and may be largely isolated, by inhibition of turbulent transfer through density clines, from any frictional coupling to the upper layer flow field. For example, in the rotating tank demonstration, if the water were stratified, dye placed very close to the top of the moving object would follow the movement, while dye placed near the water surface would remain in place. Huppert and Bryan (1976) used a numerical model to investigate the evolution of a stratified Taylor column over a small bump in the sea floor. At the initial impingement of a current flow on the bump, relatively heavy water is raised upward by the flow over the bump. This results in higher fluid pressure at the top of the bump, which at some point exerts a pressure force sufficient to oppose any further flow onto the bank. Meanwhile, the pressure force directed radially outward from the bank comes into balance with Coriolis forces via an anticyclonic (i.e., clockwise in the northern hemisphere, anticlockwise in the southern hemisphere) circulation around the high pressure center and thus around the bank, such that no flow crosses the bank in the lower layer (Figures 2a & 2b).

Dooley (1984) analyzed records from current meters moored on the flanks of Rockall Bank, and demonstrated the anticyclonic flow 'signature' characteristic of a Taylor column. Rockall is an isolated bank off northwestern Scotland, some 370 km from the Outer Hebrides. The area shallower than 250 m is about 300 km by 100 km in size, but the bank lies mostly deeper than 100 m except in a small area near Rockall Island. The bank is the site of important demersal fisheries, and the stocks, particularly haddock, exhibit great variability in year class strength. The local haddock stock appears to be distinct from nearby North Sea stocks, despite a pelagic larval stage of up to four months. Dooley suggests that confinement of the water mass over the bank by the Taylor column effect is an important factor in maintaining the population. Large amplitude variability observed in the strength of the circulation around the bank, and corresponding changes in water properties, suggest intermittent breakdown of the Taylor column flow structure, accompanied by episodic replacement of the waters over the bank. Dooley advances the hypothesis that interyear variability in these phenomena may govern recruitment variation in haddock and other demersal fishes.

An interesting aspect, which (to this writer's knowledge) has not yet been specifically addressed, is the likelihood of continued local enrichment of the trapped water volume by frictionally-driven upwelling. Note that the part of the flow around the bank that is directly adjacent to the bank surface will be retarded, relative to the main anticylonic circulation, by friction. Thus the Coriolis force is lessened with the result that the pressure gradient force directed radially outward from the bank is no longer balanced locally. The result should be lower order flow directed horizontally outward from the bank (Figure 2c). Under certain circumstances (e.g., more stable stratification above the level in question, etc.), it is possible that some upwelling along the flanks of the bank might be induced (Fig. 4, white arrows), from which dissolved nutrients could be diffused into the trapped region over the bank. The other possibility is that the frictional outflow would be supplied from the layer above the bank surface; in that case the effect could be similar because the resultant draining away of the pressure head could allow the incident large scale flow to lift more relatively dense, nutrient-enriched deeper water onto the bank to reestablish the Taylor column balance (Fig.4, black arrows). The specifics of these processes merit theoretical investigation, as they regulate the character of flow through the trapped volume, i.e., the balance between local enrichment of larval habitat and loss of entrained larvae. They also may have connotations for such ecological problems as "Darwin's question" (Andrews & Gentien,1982), "the island mass effect" (Doty & Oguri,1956), etc. For example, they might be important in providing nutrient enriched water to the vicinity of a reef edge where it might be available for uplift and supply to the reef surface by more local mechanisms such as discussed by Wolanski & Picard (1983) and Thompson & Wolanski (1984). In a somewhat deeper oceanic situation, Genin & Boehlert (1985) found higher chlorophyll concentrations where domed isotherms over Minami-kasuga Seamount (260 m minimum depth), resembling Taylor column effects, penetrated into the lower euphotic zone.

A very attractive aspect for experimental efforts is the well defined and apparently readily monitored anticyclonic flow 'signature' associated with these structures. Dooley (1984) has shown that it is possible to extract reasonable intepretations from near-bottom current records from as few as two locations on opposite flanks of the bank. Bottom-moored continuously recording meters seem ideal, but the recent development of various types of acoustic, expendable, or inexpensive and easily deployed retrievable current profiling instruments might provide some alternative methodologies. The characteristic temperature doming can be easily measured by standard bathythermograph sections, etc., but unfortunately existence of such doming is a necessary, but not a sufficient, condition for a 'trapped' Taylor column type of structure. In a case where its existence is demonstrated, the well defined and understood, organized nature of such a structure would simplify investigation of the associated biological effects, e.g., a restricted sampling of vertical distributions might substitute for full three-dimensional coverage.

How likely are such effects in tropical demersal habitats? At present we have no definite answer to the question. Certainly, in equatorial regions the Coriolis constraint becomes weak, and such vorticity-dependent hydrodynamic structures would seem less likely. This might be conteracted to some extent in those tropical areas where storm-forced flow variability, capable of disrupting the structures, may be less frequent and intense. There are certainly major tropical reef areas which are not in the immediate vicinity of the equator. The geostrophic flow relationship, which likewise depends on the Coriolis constraint, is considered to hold to a reasonable degree to within several degrees latitude of the equator (e.g., Montgomery & Stroup,1962). This problem is one where investigation via the comparative scientific method might be particularly effective, e.g., one might look for patterns in species composition, and (where information can be generated) apparent recruitment variability and rate, etc., as functions of distance from the equator, stratification, dispersal-related adaptations, etc.

Many tropical demersal habitats are characterized by particularly shallow, irregular topography related to coral structures; thus frictional effects might seem to disrupt the simple dynamic balances associated with an ideal Taylor column. However, one expects such quasi-geostrophic hydrodynamic features to be of rather large scale in any case. We would therefore expect the essential circulation to be located over the deeper flanks of the banks; in this case the shallow areas would constitute the trapped regions of no net large scale flow, and local frictional effects would be irrelevant. In fact the basic mechanism could apparently act around single large islands, groups of islands sharing a common subsurface topographic feature, etc., whenever a local horizontal fluid pressure 'high' becomes established at the feature and the scale is large enough that rotational effects dominate the frictional effects. Note that Rockall Bank, the site of Dooley's suggestive findings, does itself break the surface in one location.

4. HYPOTHESIS: RECRUITMENT REGULATION BY TOPOGRAPHICALLY-TRAPPED HYDRODYNAMIC STRUCTURES

The hypothesis that recruitment variability may be governed by variations in ocean flow conditions affecting local retention of larvae is of course neither novel nor new (e.g., Hjort,1926; Walford,1938; Johannes, 1978). However, it has sometimes been viewed in terms of variations in the transport of the bulk of the larvae. Of course, because of the enormous reduction in numbers from the time of hatching to the time of recruitment, what happens to the average larvae, or to 90 percent of the larvae, or even to 99.9 percent of the larvae, may be irrelevant. The considerations presented above suggest the possibility that even a relatively small fraction of the larvae, contained locally in some type of trapped hydrodynamic structure, etc., could be the major source of local recruitment. This in turn implies that the bulk of the larvae, drifting in the upper layers or elsewhere, may have little or no prospect at all of experiencing eventual recruitment although they would serve the important function of maintaining the possibility of chance re-establishment of the species in distant, and presumably rare, situations where local extinction may have occurred. And it is perhaps discomforting to realize that in such a case, painstaking efforts to define variability in distributions, concentrations, probable trajectories, etc., of this 'bulk of the larvae', could be useless in attempting to account for observed recruitment variability.

Thus, we might adapt Dooley's (1984) hypothesis to tropical reef/bank systems by (1) including the possibility of a particularly beneficial effect of local enrichment of the trapped water parcel and (2) to explicitly recognize the fact that the trapped volume may be small in comparison to the volume occupied by recently spawned eggs and larvae. Whether or not the trapped structure particularly resembles an ideal stratified Taylor column over isolated topography, as depicted in Figure 2, should not be crucial; in areas of complex topography the structures might be correspondingly complex, and different spatial scales might interact in a non-simple manner. The hypothesis may therefore be stated as follows: Recruitment is largely generated from larvae which have been retained in some (perhaps locally-enriched) hydrodynamic structure which may be isolated by stratification from the surface flow field; recruitment variability is introduced by the transitory nature of the structure in reaction to "red noise" forcing by the larger ocean / atmosphere scales. The corollary is that the larvae not so contained will not enjoy substantial survival due to (1) loss, by dispersion, of the advantage of numbers in withstanding predation, (2) possible lack of local enrichment or other conditions leading to appropriate food concentrations, (3) nonlikelihood of randomly encountering suitable habitat for recruitment in a suitable time frame.

The hypothesis has appeal in that it is in accord with some particularly puzzling aspects of recruitment in these systems. For example, there are three types of adult reef fish species assemblages in the central Great Barrier Reef inhabiting nearshore, mid-shelf, and outer shelf areas respectively (Williams,

(Williams,1983a), and in fact Williams (1985) finds indications that the spatial distributions of pelagic larvae, still in the water column but approaching the recruitment stage, may also correspond to this distributional pattern. Flow conditions in this region are such that freely drifting larvae should have been spread spatially, in a well-mixed distribution, over the entire shelf during the pelagic phase (Williams, et al.,1984). One possible explanation is that larvae may be specifically adapted to special conditions in the water column which may involve important cross-shelf gradients. In such a case, differential survival could account for the observed distributions of survivors. This explanation faces the difficulty that there is large interyear variability observed in the magnitude of recruitment (Williams,1983b). If a poor recruitment were due to changes in the survival conditions in the water column, one would expect the hypothetical cross-shelf gradients to be shifted such that species of larvae which ordinarily survived to recruit on the mid-shelf, for example, would be observed to recruit either in the nearshore or outer shelf areas. Such spatial shifts are not observed. An alternative hypothesis explaining these observations is the one developed here: that the larvae which are surviving in substantial numbers to the recruitment stage are those which are locally retained in the immediate vicinity of the spawning grounds.

The hypothesis is in accord with the observed 'spikey' nature of recruitment variability in reef fishes (e.g.,Williams,1981,1983b; Victor,1983) which, incidentally, resembles that for haddock (e.g., Hennemuth et al.,1980). Occasional spikes of good recruitment may be attributable to situations where integrity of the trapped structure may have been maintained over an entire larval pelagic period; more frequent mediocre recruitment years might result when "red noise" disruptions of the flow or stratification fields may cause breakdown of the structures and dispersion of the trapped water parcels. An explanation of the generally observed non-relationship of recruitment rate to adult population size is afforded by the assumption that the occasional strong recruitments occur when some variable small fraction of the total amount of reproductive product is locally retained, with the variation in this effect obscuring the dependence on spawning stock size; note however that in this case the conclusion is not that recruitment is independent of spawning stock size, but rather that the resultant recruitment, although variably modified by these hydrodynamic effects, is in any particular situation directly proportional to the amount of spawning that occurred. Boden (1952) reports most reproductive activity in the fishes and marine invertebrates of Bermuda to be concentrated in the summer, when the overlying air is hot and humid (both effects promoting stratification), and when winds are calm (promoting both stratification and absence of wind-driven transients in the flow field). Williams et al.(1984) state that the time of release of larvae, of both scleractinian corals and fishes in the Australian Great Barrier Reef is concentrated in spring - summer (i.e., outside the trade wind season). Navaluna & Pauly (this vol.) show annual spawning of a variety of Phillippine fishes to be bimodal, with modes corresponding to periods of relaxed trade winds. Johannes (1978) presents similar examples from other locations thoughout the tropics where shallow marine fishes tend to spawn at times of year when prevailing winds or currents are weakest.

The hypothesis would seem to be in accord with the high degree of endemism exhibited by tropical reef fishes; e.g., evidence (1) that certain fishes inhabiting the small isolated Johnston Atoll are differentiated from those of the Hawaiian Islands, the logical source of external supply of larvae (Erlich,1975), (2) that even within the Hawaiian Islands, some species with pelagic oceanic larvae have genetically distinct populations around different islands (Johannes,1978), etc. It also would seem to explain decadal-scale delays in recovery of geographically isolated demersal stocks destroyed by overfishing, in spite of apparent adaptation of the affected organisms to particularly extended pelagic phases (e.g., Lutjeharms and Heydorn,1981a,1981b). The mechanism would seem also in accord with the very high degree of speciation which characterizes the fish communities of these systems. In addition to the obvious effect of promoting endemism which might lead to speciation, small scale spatial pattern in larval habitat, featuring limited highly favorable habitat space surrounded by much larger regions of unfavorable space, might favor local adaptations in adult reproductive behavior (e.g., location of spawning aggregations, etc.) to maximize possibilities of inserting adequate numbers of larvae in a particular parcel of favorable space; the benefit derived might be sufficient to promote development of mechanisms of reproductive isolation among segments of a somewhat contiguous adult population in order to protect these local adaptations.

5. STRATIFIED OR NON-STRATIFIED ?

Trapped hydrodynamic structures which are not isolated from the surface flow by stratification, e.g., 'non-stratified' Taylor column structures and various types of stationary eddies and swirls (e.g.,Johannes,1978,1981) also may constitute plausible larval retention mechanisms. Brainard & Wittmann (1985) show doming in the density structure (in the sense required for existence of a Taylor column) over Southeast Hancock Seamount, northwest of the Hawaiian Islands, to be trapped below the seasonal thermocline in summer but to extend into the surface layer in winter. Flow patterns suggested for Bermuda by Boden (1952) and for Johnston Atoll by Barkley (1972) show the anticyclonic curvature at the sea surface which might characterize non-stratified Taylor column effects. (Note that the jargon terms 'stratified Taylor column' and 'non-stratified Taylor column' specifically refer to stratification in the flow field rather than in the density field, although these fields are certainly interdependent. Accordingly, a 'non-stratified Taylor column' is one in which the characteristic circulation is similar in form throughout the water column even though the fluid may be stratified in the sense of having some degree of density stratification. A 'stratified Taylor column' is one in which the circulation pattern existing near the bottom is largely absent, or in the opposite sense, near the sea surface. Density stratification is, however, a necessary condition for a stratified Taylor column to exist.) Stationary eddies in tidal flows found in the Great Barrier Reef (e.g., Hamner & Hauri,1981; Wolanski et al., 1984) appear to be too transitory to retain larvae over the time scales required for significant recruitment effects (Williams et al.,1984).

The physics involved suggest that stratified Taylor column structures would tend to be more 'sticky' with respect to topography than their non-stratified analogues, i.e., to be more resistant to being shed from their topograpically-trapped positions by transients in the larger scale incident flow and pressure fields. Whereas the atmosphere is heated from below, the ocean is heated from above and so the stratification in the ocean tends to be particularly stable and resistent to vertical turbulent transfers of momentum and mechanical energy. Thus, where the flow field is isolated from the surface layers by substantial density gradients, it is much less subject to alteration by storm-induced transients. In addition, because of the large density difference between air and water, the local fluid pressure 'high' controlling the trapping mechanism may, in the barotropic (non-stratified) case, represent a local rise in sea surface level of a centimeter or less; thus a very small total volume of fluid need be dissipated (by mechanisms of the sort represented in Figure 2c) for the structure to become dislodged. In the baroclinic (stratified) case, because of the much smaller density contrast between surface water and sub-thermocline water, a local pressure 'high' of similar magnitude might represent vertical isotherm displacements of tens of meters, with the result that much greater volumes of water would have to be shifted for comparable alteration of the local horizontal pressure field to occur.

Areas of the ocean in which tidal mixing on the continental shelf is expected to be low enough for density stratification to prevail have been delineated by Hunter & Sharp (1983); their map is reproduced in slightly modified form in Figure 3. Thus the shallow shelf areas where bottom-trapped hydrodynamic structures, isolated by stratification from upper layer flows and disturbances, would be most likely to exist include the Caribbean and Gulf of Mexico regions, the areas off the northern, western, and southern coasts of Australia, the area around New Guinea, the Java Sea, the South China Sea, the Gulf of Thailand, the Philippines, the western portion of the Bay of Bengal, virtually the entire east and west coasts of Africa, the Iberian Peninsula and Bay of Biscay, most of the east coast of Brazil, the Peru - Humboldt Current region, and the California Current region. These are also the regions where vertical current shears associated with stratified conditions might allow vertical migratory behavior to exert substantial control on advection trajectories. Note that areas near oceanic islands and banks which are not on continental shelves, and so are not treated in Figure 3, will generally be minimally subject to tidal mixing and so can be considered as falling within the 'stratified' classification.

6. OTHER VERTICALLY-STRUCTURED FLOW AND RETENTION MECHANISMS

In addition to topographically-trapped rotating flow phenomena, of which stratified Taylor columns are an example, a variety of other mechanisms can introduce organized vertical structure into the transport fields experienced by pelagic larvae. Some of those having possibilities for interaction with vertical larval distributions in ways that might significantly affect larval retention and

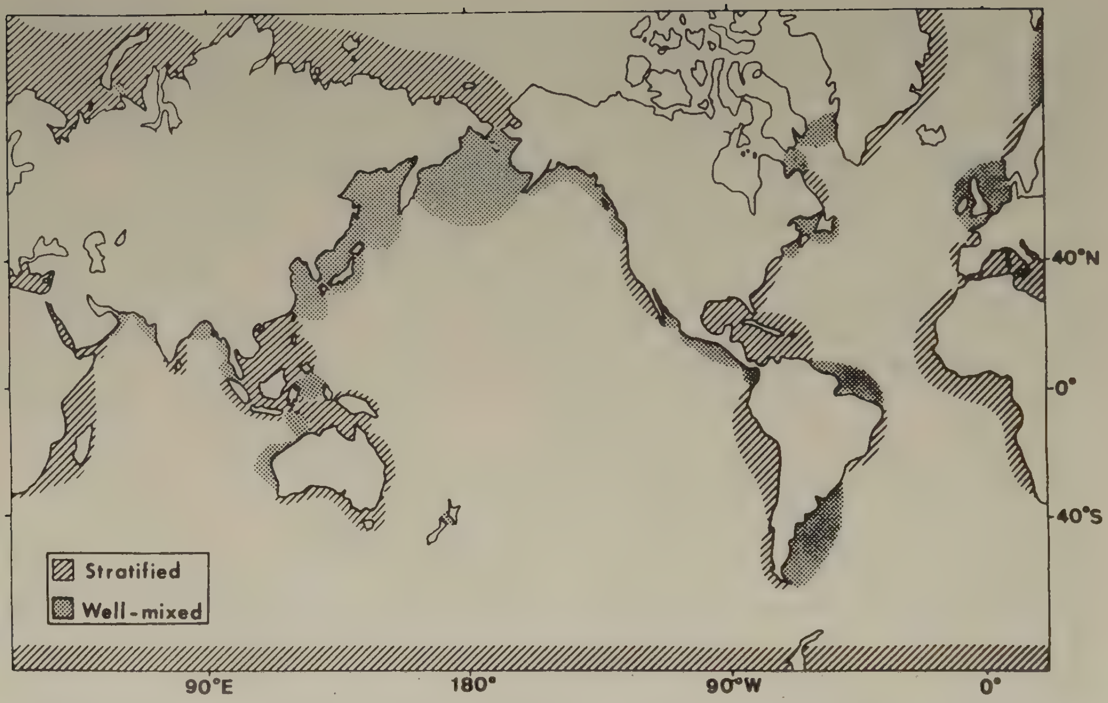
▨ Stratified
▨ Well-mixed
40°N
0°
40°S
90°E
180°
90°W
0°

Figure 3. Map of tidal dissipation in shelf areas (after Hunter & Sharp,1983). Regions of weak tidal mixing, where the water over the continental shelf is likely to be substantially stratified, are indicated by diagonally-lined shading. Regions of more intense tidal mixing, where the water over the shelves would tend to be well-mixed, are indicated by dotted shading.

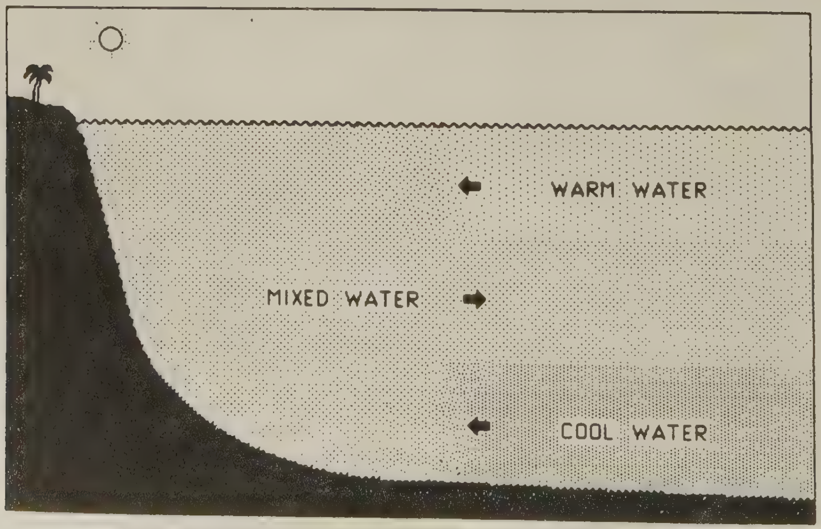
WARM WATER
MIXED WATER
COOL WATER

Figure 4. Schematic representation of the manner in which tidal mixing over shallows may induce density-driven onshore flow in the surface and bottom layers of the adjacent stratified waters, as discussed by Hunter & Sharp (1983).

6.1 Shelf sea fronts

When tidal flows over shallow shelf areas are sufficiently strong, stratification may be destroyed by turbulent mixing. When this occurs the density of the water becomes nearly constant from bottom to surface. This results in surface water of greater density, and bottom water of lesser density, over the shelf compared to water at the same depths offshore. The natural consequence is that at the offshore edge of the well-mixed region the 'lighter' offshore surface water tends to overide the 'heavier' mixed water which in turn tends to flow under the lighter water resulting in a convergent surface front; similarly at the level of the shelf bottom, the heavier offshore water will tend to flow under the mixed shelf water resulting in a convergence zone near the bottom (Figure 4). Thus larvae that maintain themselves either near the surface or near the bottom in such regions would tend to be retained in these convergent fronts. Hunter & Sharp (1981) present a rather complete review of the mechanisms and associated theory; they present a map outlining the general regions where such tidally mixed regimes, required for this type of retention mechanism, would tend to occur (shown here in Figure 3, stippled areas). Among these are the whole northeast coast of South America from Guyana to Cabo de Sao Roque, the eastern edge of the Pacific from Columbia to the Gulf of California, the region from the southern end of the Phillipines to New Guinea, Western Australia to Java, the Andaman Sea and northern Bay of Bengal, and the northern Arabian Sea.

6.2 Vertical geostrophic shears

Where the ocean is stratified, there is a tendency for the sea surface slopes which determine geostrophic surface currents to be compensated by opposite sloping density surfaces at depth. The result is variation of horizontal pressure gradients with depth and corresponding vertical shear in the geostrophic flow field. These effects are strong enough that flow near the bottom, even in shelf regions, may be opposite in direction to the surface flow. Organisms undertaking vertical migrations, such that time is apportioned among oppositely-directed flows, would be aided in maintaining geographical position. In addition, vertical migration within a flow having vertical shear has the effect of altering a planktonic organism's position relative to conditions being advected horizontally at a particular level. For example, in a horizontally patchy environment, if pelagic larvae experiencing unfavorable food concentrations were to initiate vertical migration behavior, while those experiencing adequate concentrations did not, it would lead to a greater proportion of larvae finding and remaining within favorable food patches (Doherty *et al.*,1985).

6.3 Bottom boundary layers

Directly adjacent to the ocean bottom, flow is retarded by friction. Thus an organism that settles to the bottom, or even grasps the bottom in some manner, may largely avoid advection. Organisms that undertake vertical excursions off the bottom in synchrony with oscillating tidal flows may thus experience net horizontal displacements which are very different from average flow trajectories (*e.g.*, Rothlisberg, *et al.*,1983). In large-scale, fairly long-period flows (*i.e.*, longer than a half-pendulum day, which becomes infinitely long at the equator), the effect of the earth's rotation is important, and bottom boundary flow is deflected to the left (right) of the interior flow in the northern (southern) hemisphere. This is termed a 'bottom Ekman layer'.

6.4 Surface wind drift

Present understanding of large time- (again, longer than a half-pendulum day) and space-scale transport of water in the surface layer by the direct action of the wind is based on Ekman's (1905) theory which involves a balance between vertical friction and rotational deflection (Coriolis). The fine-scale vertical structure of the Ekman velocity field depends on vertical eddy viscosity characteristics which are not well known. However the total transport of water in the layer between the sea surface and the depth at which surface wind drift becomes negligible does not depend on these characteristics, but depends merely on the stress of the wind on the sea surface and the latitude. The stress varies as the square of the surface wind velocity. The latitude dependence of the associated Ekman transport is as the reciprocal of the sine of the latitude. For example, a steady 10 m/sec wind at 10 degrees latitude induces a transport of about 6 cubic meters per second across each meter of width; at 30 degrees latitude this is reduced to about 2 cubic meters per second. This 'Ekman transport' is directed ninety degrees to the right (left) of the wind in the northern (southern) hemisphere. The depth of this 'Ekman layer' is generally considered not to exceed 100 m, and most of the transport probably occurs typically within the upper 10 to 30 m. The uppermost part of the Ekman layer moves at a lesser angle to the wind; Ekman's steady-state theory has the actual sea surface moving 45 degrees to the right (left) of the wind. Drifting objects, drogued bouys (e.g., McNally et al.,1983), etc., often exhibit trajectories which are at lesser angles to the wind, indicating contributions of flow components other than Ekman drift (see sections on Langmuir circulations and on surface wave transport, below). Near the equator, the earth's rotational effect becomes minor and the dynamic balance tends to be between vertical friction and fluid acceleration. The consequence is a tendency for upper layer movement in response to wind events to be more toward the downwind direction.

6.5 Langmuir circulations

The streaks or slicks on the sea surface that are often observed to parallel the wind direction under moderate wind conditions have been shown by Langmuir (1938) to correspond to surface convergence zones associated with a series of counter-rotating vortices, with axes oriented parallel to the wind, in the surface layer of the ocean. Leibovich (1983) presented a recent review of the phenomenon. Downwelling velocities beneath the surface convergences have been observed to be of the order of 3 to 7 cm/sec. Downwind ocean surface velocity is greater within the convergent streaks than between (indicating a possible mechanism for downward transfer of momentum supplied by the wind through a downwind-moving surface slab to a frictional Ekman layer below). Thus, organisms able to maintain themselves very near the surface are concentrated in a region of most rapid downwind transport. The circulations tend to form within a few minutes of wind onset. The depth of penetration of the cells appears to be limited to the first significant density discontinuity; there is evidence that the shape of the vortices is somewhat circular and so the penetration depth will tend to be of the order of half the distance between the surface convergences marked by the slicks.

6.6 Surface wave transport

Linear (infinitesimal amplitude) wave theory predicts movement of water particles in closed orbits which are circular in shape in deep water and eliptical in shallow water; thus no net drift of water is indicated. However, the higher order theory that describes waves of finite amplitude, features orbits which are not closed and therefore a net transport in the direction of wave advance (e.g., Philips,1977). This is commonly refered to as Stokes transport. The magnitude of Stokes transport in an inviscid fluid varies with the square of the wave height and inversely with the product of wavelength and period. Since, in deep water, orbit diameters and associated particle velocities attenuate exponentially as a function of the ratio of depth over wavelength, Stokes transport attenuates with depth in the same manner, attenuation being therefore more rapid at shorter wavelengths. For example, a wave of 2 m height, 125 m length, and 9 sec period would have an associated net forward Stokes velocity at the surface of 0.035 m/sec. At a depth equal to 1/4 wavelength, the Stokes velocity falls to less than 5% of its surface value. Over the total depth of surface wave influence, our example 2 m, 9 sec wave would have an associated forward transport of 0.35 cubic meters per second across each meter width. A shorter wave (2 m height, 25 m wavelength, 4 sec period) would generate a Stokes transport more than twice as large (i.e., 0.79 m3/sec/m). Note that waves of this height would be locally generated by winds of the order of 10 m/sec (e.g., Anon. 1951); thus the Stokes transport in a locally produced wave field would be considerably less than the associated surface Ekman transport (see above section on surface wind drift).

The effect of fluid viscosity on Stokes transport has been investigated by Longuet-Higgins (1953). Where wave-induced velocities reach the sea floor, viscous retardation due to proximity to the solid boundary acts more strongly on the lower portions of each orbit. The result is augmented forward drift along the bottom, increased in magnitude by a factor of 2.5 over that which would occur at that depth according to the non-frictional profile which describes the Stokes drift field at depth levels not directly adjacent to the bottom (Phillips,1977). A similar viscous effect causes augmentation of the stokes drift directly adjacent to the sea surface.

Although Stokes drift may be generally smaller than Ekman drift in a locally produced wave field, it is possible that Stokes drift associated with long period swell propagating from other regions (particularly from higher latitudes, etc.) into low wind situations could constitute a significant retention mechanism. Such

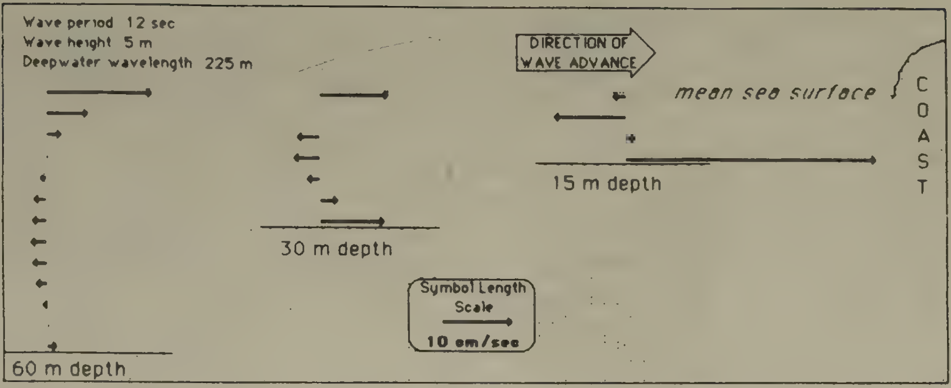

Figure 5. Vertical profiles of Stokes mass transport velocity computed according to the model of Longuet-Higgens (1953), which includes the effect of viscosity in enhancing forward transport at the sea surface and sea bottom and a return flow distributed through the water column. The example shows mass transport velocity vectors at 5-metre depth intervals under a 5 metre high, 12 second period, shoreward-directed swell in total water depths of 60, 30, and 15 metres, respectively.

long waves would begin to be refracted toward shallower water relatively early upon encountering subsurface shoaling. Wave transport in such a situation is directed invariably onshore at sufficiently shallow depths. Pressure driven rip currents, etc., which would have a more constant profile with depth, provide the offshore-directed return flow required to maintain a mass balance. Thus, organisms that maintain a position near the sea surface, or in the narrow layer of enhanced drift near the sea floor, would experience shoreward transport on average. Figure 5 provides an example of the alteration of the Stokes drift profile in shallow water, according to Longuet-Higgins' (1953) analysis of flow in a closed-ended channel where stokes drift must be balanced by an equal return flow. Although the combination of Stokes drift toward an open coast with its balancing return flow would be highly three-dimensional (rather than two-dimensional as in a narrow channel), spatially-distributed drifting larvae would tend to average out the alongshore pattern in the flow field, so the net effect would be according to the two-dimensional representation in the figure.

In the surf zone, the situation changes radically. Breaking waves push large volumns of water shoreward in violently turbulent motions which would preclude any sort of maintenance of position or orientation by small organisms. The intense mechanical battering that characterizes the surf zone would seem to make it a very poor place for pelagic larvae to survive. In fact, the necessity for minimizing the incidence of larvae being pulverized in the surf zone would seem to constitute a possible alternate explanation to predation avoidance for the adaptive value of the spawning behaviors (i.e., favoring rapid offshore transport of larvae) and seasonalities (i.e., avoiding seasons of strong winds and associated surf conditions) enumerated by Johannes (1978).

6.7 Surface slicks coupled to internal waves

Ewing (1950) described lines of surface slicks parallel to the shoreline of Southern California, which are apparently coupled to trains of long internal waves in a shallow thermocline. The orbital velocities in the upper layer, associated with the internal waves, result in lines of surface convergence parallel to the crests but lagging the crests by one-fourth wavelength. The convergence lines collect organic materials, causing damping of surface ripples and resulting visible slicks. The slicks move shoreward at about 25 cm/sec, which is near the phase speed of the waves observed. Rattray et al. (1969) describe a mechanism by which these internal wave trains are formed by tidal action at the continental shelf break. Shanks (1983) proposed this mechanism as a vehicle for return of larval crustaceans to the shallow coastal region. He showed shoreward transport of drifting objects within propagating slicks and reported concentrations of pelagic larvae of a variety of fishes and invertebrates 40 to 60 times greater at the sea surface within propagating slicks, than in the surface areas between the slicks. If Shanks' observations have widespread generality, this is apparently a mechanism by which pelagic larval stages, that have behaviors which keep them positioned within the neuston or associated with drifting objects, could be transported shoreward.

7. A FOCUS ON VERTICAL STRUCTURE

Determining complete representative vertical profiles of swimming planktonic organisms is a demanding, time-consuming process in itself (e.g., Longhurst, 1976). In addition, sampling of fish larvae in particular has usually been directed primarily toward determining total biomasses, i.e. for the purpose of estimating population size and productivity, or toward delineating seasonality and geography of spawning grounds. Thus vertical structure has often been viewed as merely an unfortunate additional complexity and a potential source of sampling error. As a result past emphasis has been on integrating vertical inhomogeneities via vertical or oblique tows. Consequentially we really have surprisingly little information as to the vertical distribution of larvae even in large well-studied fishery stocks (R.H.Parrish, pers. commun.). Efforts to develop this information seem overdue, particularly in view of recent scientific interest in the effects of vertical migration in vertically varying flow on larval trajectories (Rothlisberg,1982) and on the ability of larvae to alter their position with respect to favorable food particle concentrations (Doherty et al., 1985).

7.1 Experimental advantages

By basing experimental and observational efforts on a framework provided by our level of understanding of vertical structure in the likely physical transport and retention mechanisms, some significant economies in required effort and resources may be afforded. We have noted a tendency for many of the potential mechanisms to be either bottom-intensified, surface-intensified, or both. Rather than assembling samples of complete vertical profiles, it may be reasonable to concentrate effort on demonstrating significant differences between larval concentrations at particular key depth levels with respect to given physical mechanisms (e.g., surface vs. mid-depth, bottom vs. mid-depth, etc.). Once a pattern of relationship or non-relationship is established, the theory of natural selection would provide a powerful deductive tool since reproductive success is the determining factor in the selection process. Thus, consistent patterns of apparent biological response to vertical aspects associated with one or another of these mechanisms would be strong evidence of natural selection and therefore of important causal linkage of the mechanism to reproductive success.

While weakly swimming pelagic fish larvae might generally have relatively little active control over their horizontal distribution, they might exert considerable control on their vertical distribution. Thus directed behavioral adaptations would be able in some degree to counter certain accidental or random displacements in the vertical, with the result that observations of vertical structure might be relatively free of unrelated random patchiness or 'noise' which might obscure the signal of the response. In such a case, assembly of a representative set of samples of vertical variability would be a much less demanding exercise than, for example, assembling a representive set of samples of variability in 'bulk' population abundance, where all the various scales of spatial patchiness would have to be somehow integrated in each estimate. Thus substantial economies of effort and resources might be realized by such a shift in point of view from quantitative three-dimensional closures of various "budgets" involved, to a single-dimensional focus on the characterization of vertical relationships among organisms, environmental properties, and dynamic processes. Observation of the manner in which these relationships might vary under varying external conditions, e.g., weather, seasonality, etc., could provide a rich source of material on which to base conclusions as to (1) the nature of the mechanisms which might have controlled the natural selection leading to the observed vertical associations, and (2) the effects of variations of the external conditions on local year-to-year recruitment variability.

Moreover, the formidable problem of taxonomic identification of early life stages of tropical demersal species could perhaps be less crucial in this type of approach; the greater emphasis would be on defining the vertical position in the water column of organisms of generalized type, under various environmental conditions, rather than on the biomasses and interactions of specific community components.

7.2 Interregional comparative studies

The opportunity for application of the comparative method among different local systems appears particularly promising. Certainly, checking for lack of covariation in recruitment variability is an obvious approach to defining the scales on which the stocks may function as closed populations. (Note however that the converse is not necessarily true. Large-scale covariation might be due to some large-scale environmental variation acting similarly on a number of smaller scale closed population segments.) Characterizing the real spatial-average recruitment variability at multiple locations might be an enormous task. However, various functional dependencies intrinsic to the hypothesis that vertically-structured retention mechanisms may regulate recruitment variability (e.g., distance from the equator, isolation from external larval sources, degree of stratification, relation to large scale ocean current systems or atmospheric storm tracks, characteristic ocean wave spectra, etc.) facilitate the arraying of a variety of data, which might be available or obtainable, in a variety of different ways likely to yield informative patterns, even if actual time series of variability were unattainable. We can regard observed adaptations as being the integrated result of a great number of 'trial and error experiments' by the population, i.e. a clear 'signal' with the large amplitude, quasi-random 'noise' represented by environmental and community-structure transients having been largely filtered out. Thus if widespread consistency in biological pattern with respect to potential environmental causal mechanisms can be assumed to reflect processes of natural selection, comparative pattern recognition on local and interregional space scales, and on seasonal and selected interannual time scales, might yield much useful information that could be extremely difficult to derive via the experimental method (Bakun,1985). Note that this approach also produces insights as to the degree of similarity in the crucial dynamics of geographically-separated ecosystems which, even if we do not understand these dynamics in detail, would aid in transferring experience among systems in order to foresee the effects of human actions or natural environmental perturbations on a given system by examining the record of similar actions or events in other systems. Finally, such a comparative effort based specifically on the question of larval retention and immigration, would provide a useful framework for addressing the basic ecological question of whether, and under what conditions, the population dynamics of tropical reef/bank fishes is controlled primarily by community interactions or by recruitment variability.

7.3 Multidisciplinary scientific effort

The class of problems treated in this paper may provide a framework for focusing efforts of a particularly broad range of marine scientific specialties on the problem of recruitment in tropical demersal systems. For example, previous interest of physical oceanographers in stratified Taylor column phenomena has been directed primarily toward the effect of these processes on the larger-scale ocean responses which are evident to humans in a more direct manner, rather than on the actual details of the processes themselves which may affect humans primarily through their affects on biological populations. Certain aspects needing theoretical investigation are mentioned above; opportunities certainly exist for important contributions from theoreticians and numerical modelers on various other aspects of the interactions of hydrodynamic and biological vertical structures. Large-scale descriptive oceanographic and meteorological input would be a crucial component of interregional comparative studies. Bottom-intensified transport processes would tend to leave identifying 'signatures' in sediment deposition patterns, affording an opportunity to enlist geological oceanographers in the effort. Of course, strong roles for biological oceanographers, ecologists, ecological modelers, sampling gear engineers, etc., are implied.

7.4 Socio-economic implications

In addition to addressing the causes for temporal variation in recruitment success, research activity on the class of hypotheses discussed here has the particular advantage of treating the extremely important question of the spatial scale on which recruitment may be generated; i.e., the scale on which a local situation may or may not function as an 'open' or 'closed' system (Roughgarden, Iwasa & Baxter,1985). For example, in an open system, local over-exploitation may not have serious consequences on subsequent recruitment since recruitment is largely generated from larvae arriving from outside of the system. However, in a closed system, local recruitment is generated largely from local spawning, and there is a much stronger argument against local over-fishing. Therefore any incremental increase in understanding of the nature and effect of larval retention mechanisms could have value in terms of the basic way in which stock / recruitment issues in tropical demersal systems are viewed, even if detailed quantitative predictive capability were not a direct outcome. This in turn could have important effects on fundamental attitudes toward industrial investment, management and conservation, by illuminating the international, national, and local 'common property resource' aspects (Glantz,1983) of tropical dermersal biological communities. Addressing such basic oceanographic and ecological scientific issues under a framework having direct social-economic implications is in accord with the dual "importance of OSLR for the development of marine science, integrating various biological and physical disciplines and various laboratory programmes around the world, in such a way as to serve the national interests of coastal states" (Anon. 1985).

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FIBROPAPILLOMAS IN HAWAIIAN GREEN TRUTLES

(This note is based on a presentation given by the author at the 6th Annual Workshop on Sea Turtle Biology and Conservation in Waverly, GA, USA. A presentation by Lew Ehrhart covering tumors in green turtles in east Florida was given during the same session).

Neoplasms identified by the Registry of Tumors in Lower Animals (RTLA) as fibropapillomas are being commonly found on green turtles in the Hawaiian Islands. Up to 10% of the nesting females tagged each year at the principal breeding colony of French Frigate Shoals have these epithelial growths ranging from a few millimeters to 30 cm in diameter. They most frequently occur on the neck, eyes, flippers, jaw, tail and sometimes even in the mouth. In Hawaii, fibropapillomas have been recorded in turtles as small as 45 cm juveniles to adult males and females over 85 cm. However, none have been found in turtles 35-45 cm, the minimum size range at which recruitment to the benthic habitat takes place in Hawaii.

During 1985, 35% of the 51 stranded green turtles examined throughout Hawaii had fibropapillomas. Local divers and fishermen regularly report seeing afflicted turtles in coastal foraging pastures and underwater sleeping areas. Such sightings are believed to have increased considerably over the past 20 years.

Fibropapillomas in green turtles were first described nearly 50 years ago by Smith and Coates (1938). At that time, 3 out of 200 green turtles (27 to 91 kg) examined at Key West, Florida (USA) had fibropapillomas. During the same year, Lucke (1937-38) mentioned that green turtles in the Dry tortugas "not infrequently suffer from papillomatous neoplasms which may attain so great a size as seriously to interfere with their locomotion." Hendrickson (1958) stated that "occasional" green turtles nesting in Sarawak, Malaysia had ulcerated fibromas on their "throat and neck." Since the RTLA began accepting specimens in 1965 (Harsbarger 1974), fibropapillomas from green turtles have been verified from the Florida Keys (RTLA Accession Nos. 12 and 651), Hawaii (RTLA 121, 1767, 1774, 1856, 1883, 2097 and 3572), and the Cayman Turtle Farm (RTLA 3099). Jacobson (1981) reported that a "slowly increasing incidence of papillomatosis" was being studied in a breeding group of green turtles at the Cayman Farm. These growths were first noted in wild captured adults but later developed in farm reared turtles. According to Jim Wood, the problem no longer exists, although several juvenile turtles released from the farm were recaptured a year or two later and found to have growths. In east central Florida, immature green turtles have been reported by Lew Ehrhart to show a high incidence of these fibrous growths during recent years where none had been seen since tagging studies began there in 1977. Pat Wells, working in the Florida Keys, has found similar growths on five of nine stranded green turtles handled during the first 3 months of 1986. Previously, only two cases had been reported out of six strandings of green turtles seen since 1982.

Thus far, the green turtle is the only sea turtle that has been documented to have fibropapillomas, although Jack Frazier and Tom Fritts have seen what were believed to be these growths in olive ridleys in the eastern Pacific.

Fibropapillomas in Hawaiian green turtles can result in reduced vision, disorientation, blindness, physical obstruction to normal swimming and feeding, and an apparent increased susceptibility to parasitism by the marine leech, *Ozobranchus branchiatus*. Observations in Hawaii also suggest that fibropapillomas can cause severe emaciation, increased predation by tiger sharks and humans, and probably a reduced ability to migrate and breed successfully. Entanglement in fishing line and other gear also appears to be more likely in afflicted turtles.

The etiology of fibropapillomas in green turtles remains unknown. Possible causes suggested in the literature include an immune response to trematode ova, secretion of hirudin by marine leeches, viruses, excessive solar radiation, chemical pollutants that impair the immune system, stress, and a genetic predisposition to neoplasia. Biopsy material from fibropapillomas on two Hawaiian green turtles was sent to the RTLA for electron microscopy, but no virus was found.

John Harshbarger of the RTLA believes that the only substantive evidence for any of the suggested causes is the consistent presence of ova from digenetic blood flukes (Family Spirochidae) within the fibrotic portion of the lesions. Smith and Coates (1939) originally reported ova in over half of the 250 fibropapillomas examined from at least six turtles. At least 7 of the 10 RTLA cases contain ova (RTLA 12, 121, 1767, 1774, 2097, 3099, and 3572), including specimens from Florida, Hawaii, and the Cayman Turtle Farm. Turtles from the latter source were heavily infested with the cardiovascular fluke, *Learedius learedi* (Greiner et al., 1980) and some of their shed ova had lodged in dermal capillaries (Jacobson 1981). The gradual increase in the incidence of fibropapillomas in captive animals suggested an infective process. In histological sections, the ova generally appear as oval, yellowish/brown, acellular capsules containing undifferentiated cells. Host response consists of a capsule of epithelioid macrophages surrounded by fibrosis. If trematode ova are in fact the etiologic agents, then the lesions represent a nonneoplastic host response, characterized by an exuberant, cutaneous, foreign body fibrosis associated with pappillary epidermal hyperplasia (John Harshbarger, pers. comm.).

The growth rate of fibropapillomas has been documented in two Hawaiian green turtles. A nesting female with no signs of neoplasia when first seen was recovered 3 years later in an emaciated stste with a large (10 X 20 cm) fibropapilloma along the dorsal base of its tail. Another apparently healthy tagged turtle, an adult male, had numerous growths, including a 10 cm diameter mass in the axilla, when seen again just 2 years later. The fact that relatively small turtles in Hawaii can be heavily infested with fibropapillomas indicates that growth can occur fairly fast under certain conditions.

The experimental treatement of fibropapillomas in Hawaii has included surgical removal and strangulation. Neither procedure proved satisfactory due to the large number of growths often present, their highly vascular nature when large, and the apparent presence of nerve bundles that transmit pain, especially in growths associated with the eyes. There is no evidence to suggest that fibropapillomas in

Hawaiian turtles may cease or diminish spontaneously.

The Hawaiian population of green turtles is geographically isolated and relatively small, with only a few hundred females nesting annually at French Frigate Shoals. A recovery team has recently been appointed to formulate a plan to rehabilitate the population. The occurrence of fibropapillomas is viewed as one of several problems that urgently need to be addressed through addtional research. In general, the problem of disease is an area in which basic data are frequently lacking and more attention is needed for the development of effective management plans. Workers are therefore encouraged to document any occurrence of neoplasia found in sea turtle populations by submitting preserved tissue to the RTLA, The Smithsonian Institutuion, Room W216, Washington, DC 20560 USA.

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Ontogenetic Changes in the Plastron Pigmentation of Hatchling Hawaiian Green Turtles

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Hatchling green turtles, *Chelonia mydas,* differ from the young of other sea turtles by their sharply contrasting white plastron and dark carapace. Except for the Australian flatback, *C. depressa,* hatchlings of other sea turtle species have a predominantly dark plastron. According to Bustard (1972), hatchling green turtles are "blackish above and immaculate white below." This countershading is believed to serve as camouflage from avian and fish predators while the turtles are floating at the surface in pelagic habitat (Carr, 1969). The black dorsum is also considered to have adaptive significance by elevating body temperature, hence metabolism, through the absorption of solar radiation (Bustard, 1970). No explanation has been offered as to why other hatchling sea turtles are not similarly countershaded, since they also pass through a pelagic phase.

According to Hirth (1971), dorsally the neonatal green turtle is black to dark brownish, or greenish black, with white edges to the carapace and flippers. Ventrally the plastron is white with black at the ends of the flippers, but with white edges. Except for differences in size (ca. 4–6 cm carapace length), only minor variations in the appearance of hatchlings derived from widely separated nesting beaches have been recognized in the literature. Pritchard (1979) alone has indicated that the white underside of the hatchling green turtle sometimes has a dark band of pigment along the marginal scutes, which is said to vary in intensity from one population to another. However, this characteristic may not be very common, since no other authors have mentioned it. No pigment is present along the ventral surface of the marginal scutes of hatchlings examined from Hawaii (Balazs, 1980), nor in those from Tortuguero, Costa Rica which have been deposited in the Florida State Museum (J. Mortimer, pers. comm.).

The available literature indicates that the plastron of the post-hatchling green turtle remains nearly white throughout growth and development. For example, Hughes (1974) states that all underparts, except the flippers, remain white as green turtles from South Africa grow from hatchlings into 20 cm juveniles. From 20 cm to adult, the plastron is reported to only change from off-white to yellow. Pritchard (1979) also indicates that the plastron stays light colored, merely becoming pale yellow in the adult instead of pure white. However, the pigmentation previously mentioned by Pritchard (1979) along the underside of the marginal scutes "may be intensely black in juvenile Ascension turtles." Similar pigmentation is evident in a captive reared 7.5 cm juvenile from Australia shown, but not described, in Glazebrook (1981). However, it is only faintly present on a 6.5-cm sibling shown in the same paper. Though not stated by Pritchard (1979), it can be assumed that green turtles from Ascension eventually lose such pigment, since it has not been described in larger turtles from this location. Jeanne Mortimer (pers. comm.) recently examined 75 young green turtles from Ascension Island preserved at the Florida State Museum. They ranged from hatchlings to 12 cm juveniles. She confirmed that on the venter the marginals alone are dark in the hatchlings, and this dark pigmentation fades when the juveniles reach 8 to 10 cm in carapace length.

The purpose of this present note is to document and describe a radical color change that occurs in the plastron during the early life stage of the Hawaiian green turtle. Except for brief mention in Balazs (1980), a transition of this nature has not been reported elsewhere in the literature. The plastron and underside of the marginal scutes of neonatal (5 cm) green turtles from Hawaii are white, but by 6 cm become diffused with black and gray pigment. The pigment reaches its greatest intensity at about 7–8 cm. Thereafter, it fades away and usually disappears completely by 13 cm or less, when the undersurface returns to complete white. The three major stages of this pigment transformation are shown in Fig. 1. The formation and subsequent dissipation of dark pigment are entirely dependent on the size of the turtle, and not on its age. Consequently, faster growing turtles pass through the pigmented phase more rapidly than siblings growing at a slower rate. This point has been confirmed through captive rearing of more than 300 hatchlings from Hawaii since 1972 under different dietary and environmental conditions. The pigment changes have not, however, been documented in free ranging turtles, since there have been no opportunities to do so. As elsewhere, Hawaiian green turtles in this size range are almost never seen in the wild, and are presumed to be living in pelagic habitat. In Hawaii, green turtles are absent from nearshore habitat until they reach 35 cm or more.

It is unknown if this color change is unique to Hawaiian green turtles, or has simply been overlooked in certain other populations. For many populations, hatchlings have undoubtedly not been reared in captivity to carefully record ontogenetic changes. Even where captive rearing has occurred, there is a human tendency to focus attention on the dorsal more readily visible surfaces of young turtles held in tanks. Pigment along the marginal undersurfaces of juvenile Ascension green turtles mentioned by Pritchard (1979), and Australian ones shown in Glazebrook (1981), indicate that color changes do occur to some degree in other populations. However, no literature reports have shown or suggested it to be as pronounced as reported herein for the Hawaiian population.

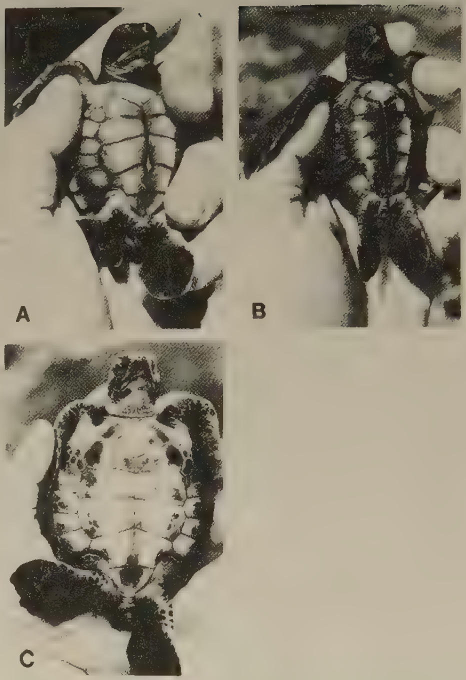

FIG. 1. Changes in the plastron pigmentation of the Hawaiian green turtle. A. Beginning of dark pigment at 5.8 cm carapace length (2 weeks old). B. Intense dark pigment at 7.0 cm carapace length (4 weeks old). C. Dissipation of dark pigment at 11.2 cm carapace length (16 weeks old).

In the eastern Pacific, the taxonomy of *Chelonia* has not been resolved. The name "black turtle" is commonly used for this markedly different form. Scientific names referring to the black turtle have included *Chelonia agassizi, C. mydas agassizi,* and *C. mydas carrinegra.* Mature adults are characterized by their black carapace and other dark dorsal surfaces, and large blotches of gray pigment throughout most of the plastron and ventral marginal scutes. However, almost nothing has been written about plastron coloration in the hatchling or juvenile black turtle of the eastern Pacific. Caldwell (1969) stated that hatchlings of the *mydas* form could not be distinguished from the black turtle, so presumably the latter also has a completely white underside. In 1980, Archie Carr at the University of Florida raised a single black turtle hatched in the laboratory from an egg acquired at Maruata Bay, Michoacan, Mexico. As a neonate, the ventral surface of this specimen was reported to be completely white. Dark pigment subsequently developed in a manner similar to what has been described for the Hawaiian green turtle, but not as intense at its darkest point. At 15 months of age (18–20 cm) this turtle still had considerable dark pigment (K. Bjorndal, pers. comm.). However, according to Archie Carr (pers. comm.) fading had started to occur when it died several months later. The turtle is preserved in the Florida State Museum, Gainesville.

It is unknown what adaptive value, if any, may accrue from dark pigmentation occurring in the ventral surface of 6 to 9 cm Hawaiian green turtles. A similar phenomenon appears to take place in eastern Pacific black turtles and possibly other populations of green turtles. More work is needed to elucidate this point, and others, by simultaneously rearing groups of hatchling green turtles from different locations under similar environmental conditions.

Acknowledgments.—Appreciation is extended to Jeanne Mortimer, Archie Carr, and Karen Bjorndal for contributing unpublished information and helpful suggestions for the preparation of this note.

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RESUSCITATION OF A COMATOSE GREEN TURTLE

Fewer sea turtles would drown from incidental capture in shrimp trawls and other fishing gear if better resuscitation procedures were used. The current recommended practice is to hold a comatose turtle out of water in either a prone or supine position, and see if it revives over a period of 1 to 24 h. The turtle's posterior should be elevated if held prone. If placed on its back, the plastron should be periodically compressed ("pumped") by hand or foot (Hopkins and Richardson 1984). The actual manner in which these manipulations may foster resuscitation has not been described. Presumably they are aimed at ventilating the lungs, draining water from the respiratory passages and lungs, and promoting cardiovascular function. It is unknown what percentage of comatose turtles are revived, or what the survival rate of revived turtles is following release. From the high frequency of beach strandings adjacent to certain shrimp trawling areas, considerable mortality apparently takes place (Shoop and Ruckdeschel 1982), although it is not known whether attempts were made to resuscitate these turtles.

The resuscitation of a comatose green turtle, *Chelonia mydas*, at Johnston Atoll (lat. 16°45'N, long. 169°31'W) in November of 1983 provided a new perspective on the problem, and suggested the use of additional therapy. During a tagging study employing large mesh nets in algal foraging pastures, an entangled subadult green turtle (68 kg, 76 cm carapace length) became snagged on coral 2 m deep making it unable to surface. The seawater temperature was 27.5° C. The turtle was submerged for at least 30 min before emergency retrieval could be carried out from a small boat. When it was brought to the surface there were no signs of life except for contraction of the tail when extended manually. The turtle was placed on its back and the plastron pumped every 2-3 min for 1 h following rescue, but no resuscitation was evident. Upon close examination, it was determined that the movement of air caused by pressing on the plastron was only taking place into and out of the esophagus, and not the trachea. At all times the glottis, a longitudinal slit posterior to the tongue, remained tightly shut and could only be opened by forcing a finger into it When the finger was withdrawn, the glottis immediately returned to the closed position. To hold the glottis open and permit the passage of air, a 40-cm piece of 10 mm outside diameter, 7 mm inside diameter, plastic tube was inserted 2 cm. With the turtle prone, the lungs were then ventilated by gently blowing into the tube at irregular intervals over the next hour No water drained out through the tube, although fluid apparently from the stomach came out of the mouth. After being seemingly lifeless for over 2 h, the turtle suddenly raised its head well into the air and took a deep breath. For the next 30 min distinct breaths gradually became more frequent and the tube was finally removed. Movement of the flippers also gradually resumed. The turtle was left prone for the next 11 h in a confined area. In the morning it was found active and appeared fully recovered. A large quantity (1.5 kg) of voided feces was present. When released, the turtle swam a short distance near the surface, took a breath, and dove out of sight in a normal manner

Dead green turtles of various sizes which I have examined have all shown a closed glottis, like the comatose specimen reported here. This appears to be the normal state, serving to prevent the inhalation of seawater The glottis appears to open only with the outward movement of the hyoid apparatus and gaping of the mouth to take a breath Closure of the glottis in the green turtle, or any other sea turtle species, has not been previously mentioned in connection with resuscitation efforts. If the goal is to ventilate the lungs, then an open air passage must be established. The insertion of a small plastic tube is a simple and convenient way to meet this objective. In addition, since the lungs are located dorsally, under the carapace, the prone position for resuscitation would seem best to avoid compression from the heavy food-laden digestive tract and other organs

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THE 1985 SPAWNING BIOMASS OF THE NORTHERN ANCHOVY

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ABSTRACT

The 1985 spawning biomass of the central subpopulation of the northern anchovy (*Engraulis mordax*) is 522,000 metric tons (MT). This estimate was made using the egg production method, which computes the spawning biomass as the ratio of the daily egg production rate (eggs per day for the entire population) and the daily specific fecundity (eggs per day per metric ton). For the entire population, the egg production rate was 16.95×10^{12} eggs/day, and the daily specific fecundity was 37.00×10^{6} eggs/day/MT. In 1985 anchovy eggs were found farther offshore than in any survey since the egg production method was first employed in 1980. A significant number of eggs spawned far offshore may have been missed by the survey, thus biasing the estimate downward.

RESUMEN

En 1985, la biomasa de desove de la subpoblación central de la anchoveta norteña (*Engraulis mordax*) es 522,000 toneladas métricas (TM). Esta estimación fue calculada por medio del método de producción de huevos, él cual calcula la biomasa de desove como la proporción entre la tasa diaria de producción de huevos (huevos por día para toda la población) y la fecundidad específica diaria (huevos por día por tonelada métrica). La tasa de producción de huevos de la población total fue 16.95×10^{12} huevos/día, y la fecundidad específica diaria 37.00×10^{6} huevos/día/TM. Los huevos de anchoveta fueron encontrados más alejados de la costa en 1985 que en cualquiera de los estudios anteriores desde que el método de producción de huevos fuera inicialmente empleado en 1980. Es posible que un número significativo de los huevos puestos mar afuera haya sido obviado por el presente estudio implicando una subestimación de la biomasa.

INTRODUCTION

This estimate of the 1985 spawning biomass of the central subpopulation of the northern anchovy (*Engraulis mordax*) fulfills the requirements of the Anchovy Management Plan adopted by the Pacific Fishery Management Council (PFMC 1983). In the past, anchovy biomass has been estimated using a larval census method (Smith 1972; Stauffer and Parker 1980; Stauffer and Picquelle 1981) and an egg production method (Parker 1980; Stauffer and Picquelle 1980; Picquelle and Hewitt 1983, 1984; Hewitt 1984; Lasker 1985). In 1985 only the egg production method was used to estimate the anchovy spawning biomass.

With the egg production method (EPM), we compute the spawning biomass as the ratio of the daily production of eggs (eggs per day for the entire population) and the daily specific fecundity (eggs per day per metric ton) of the adult population. The daily production of eggs is estimated from the density and embryonic developmental stages of egg samples from an ichthyoplankton survey. The developmental rates of anchovy eggs are measured in the laboratory under various temperature regimes. The daily specific fecundity of the anchovy population is estimated from adult fish sampled during a trawl survey. The parameters used to produce the average specific fecundity are average female weight, batch fecundity, sex ratio, and the proportion of females spawning each night. Variance and covariance values are also produced for the parameters.

The survey results, the EPM estimate of spawning biomass, and the variance of the estimate are presented in the following sections.

DESCRIPTION OF THE SURVEY

The 1985 EPM survey of the central subpopulation of northern anchovy was conducted with the NOAA ship *David Starr Jordan* from January 28 through March 8, 1985. The survey (Figure 1) ran from north to south starting approximately 50 miles south of Monterey, California, (CalCOFI line 71.7) and ending at Bahía del Rosario, Baja California, (CalCOFI line 110.0). Several survey lines were extended farther offshore than planned because of the unexpected extent of positive samples. The survey lines directly north of the greatest concentration of anchovy eggs (northwest of San Diego) may not have extended far enough offshore to sample the northern extent of this concentration. Thus a significant number of anchovy eggs may have been missed.

We used a 25-cm-diameter vertical egg net with a 0.15-mm mesh to take plankton samples from 70-m-

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[Manuscript received January 29, 1986.]

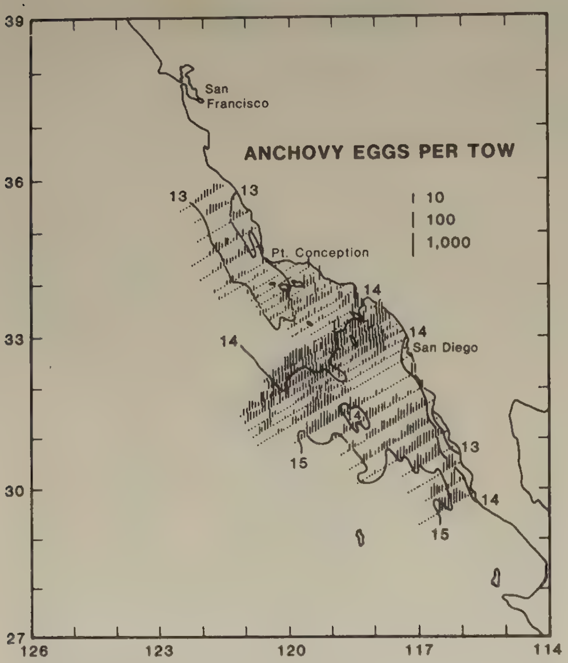
ANCHOVY EGGS PER TOW
10
100
1,000
San Francisco
Pt. Conception
San Diego
13
13
14
14
14
15
13
14
15
39
36
33
30
27
126
123
120
117
114

Figure 1. Geographic distribution of ichthyoplankton stations, anchovy eggs, and surface isotherms.

deep water at 492 stations, and 210-m-deep water at 417 stations. Of these 809 samples, 547 contained anchovy eggs (Figure 1). A 15-m^2 pelagic trawl with a 2-mm-mesh liner was towed at 74 stations. Adult anchovies were caught at 64 stations (Figure 2). (For a more complete description of the field operations, see Cruise Report 8502-JD, dated April 29, 1985, William Flerx, Southwest Fisheries Center, La Jolla, California.)

Anchovy eggs extended much farther offshore than in any other year since egg production surveys began in 1980. Spawning activity, as in previous years, was correlated with sea-surface isotherms (Lasker et al. 1981) (Figure 1). South of Point Conception, spawning was generally constrained within the 15°C isotherm. North of Point Conception, spawning occurred in colder water. The cruise report of the USSR research vessel *Mys Babushkina* (Cruise Report 8503-MB, dated June 7, 1985, D. Abramenkoff, Southwest Fisheries Center, La Jolla, California) gave quantitative evidence of spawning in the area north of our survey area up to the San Francisco Bay area (Figure 3). On the Soviet cruise, ichthyoplankton samples were visually "scanned" (the number of larvae per tow roughly estimated) to estimate the number of anchovy larvae taken at each station. We used the scanned estimates to estimate the anchovy spawning biomass in the area north of our survey.

In summary, in the late winter of 1985, anchovies were spawning from Baja California to the San Francisco Bay. This spawning was concentrated in the Southern California Bight and extended farther offshore than usual. Because some of our survey lines may not have extended far enough offshore, many anchovy eggs may not have been counted. This would bias our biomass estimate downward. South of San Diego and north of Point Conception the population was closer to shore, but generally not present in the colder, upwelled water adjacent to the coast.

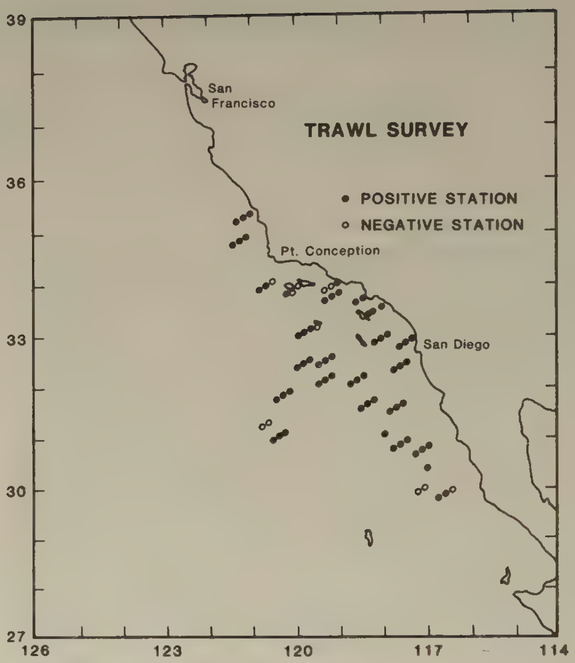
TRAWL SURVEY
● POSITIVE STATION
○ NEGATIVE STATION
San Francisco
Pt. Conception
San Diego
39
36
33
30
27
126
123
120
117
114

Figure 2. Geographic distribution of trawl stations.

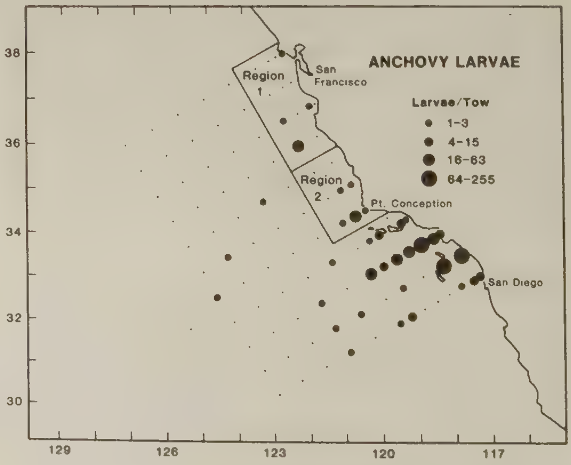
ANCHOVY LARVAE
Larvae/Tow
1-3
4-15
16-63
64-255
Region 1
Region 2
San Francisco
Pt. Conception
San Diego
38
36
34
32
30
129
126
123
120
117

Figure 3. Geographic distribution of ichthyoplankton stations and anchovy larvae from the Soviet cruise (*Mys Babushkina*).

BIOMASS MODEL

The egg production method estimate of spawning biomass (Parker 1980; Stauffer and Picquelle 1980) is:

$$B = PA\frac{k\,W}{R\,F\,S} \qquad (1)$$

where B = spawning biomass in metric tons,
P = daily egg production rate in number of eggs per day per 0.05 m^2,
W = average weight of mature females in grams (g),
R = female fraction of the population by weight,
F = batch fecundity in number of eggs,
S = fraction of mature females spawning per day,
A = area of survey in units of 0.05 m^2, and
k = conversion factor from grams to metric tons (10^{-6} MT/g).

An estimate of an approximate variance for the biomass estimate, derived using the delta method (Seber 1982), is:

$$\mathrm{var}(B) \cong B^2\{\mathrm{var}(P)/P^2 + \mathrm{var}(W)/W^2 + \mathrm{var}(R)/R^2 + \mathrm{var}(F)/F^2 + \mathrm{var}(S)/S^2 + 2[\mathrm{cov}(PW)/PW - \mathrm{cov}(PR)/PR - \mathrm{cov}(PF)/PF - \mathrm{cov}(PS)/PS - \mathrm{cov}(WR)/WR - \mathrm{cov}(WF)/WF - \mathrm{cov}(WS)/WS + \mathrm{cov}(RF)/RF + \mathrm{cov}(RS)/RS + \mathrm{cov}(FS)/FS]\}.$$

DAILY PRODUCTION OF EGGS

The daily production of eggs in the sea, P, is the number of eggs spawned per night per unit area (0.05 m^2, the area of the ichthyoplankton net) averaged over the range and duration of the survey. The density of eggs was determined from an ichthyoplankton survey, and the embryonic developmental stage of each egg was determined by microscopic inspection. The ages of the eggs in hours from spawning were computed from the embryonic developmental stage by a FORTRAN program (Hewitt et al. 1984; Lo 1985) which assumes that the daily spawning of anchovy eggs occurs at 2200 hours. An exponential mortality curve for the eggs was fit to the egg age data. I estimated the daily production of eggs as the value of the predicted curve at the time of spawning.

In order to reduce the variance of the estimate of P, I used a two-step sampling scheme with postsurvey stratification. The first step was the systematic ichthyoplankton sample of the survey area. Each sample was assigned a weighting factor proportional to the area the station represented. The second step was to divide the survey area into two strata: stratum 1 was defined as the area where eggs were found or were likely to be found based on incidence in surrounding locations, and stratum 0 was the area devoid of eggs (Figure 4).

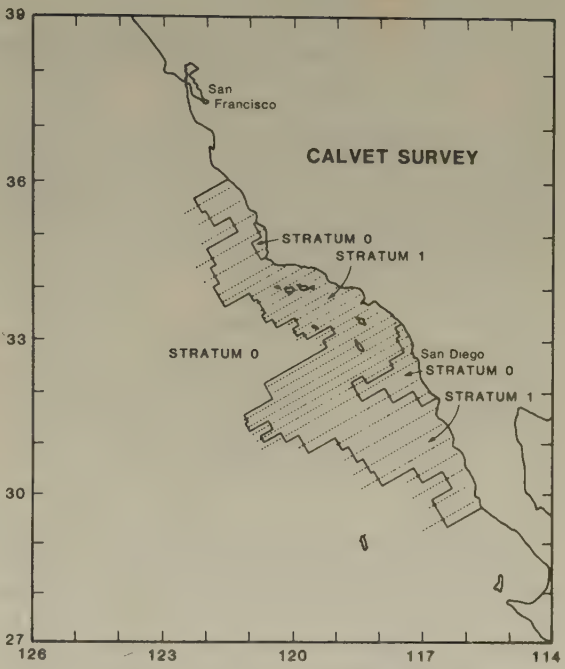

Figure 4. Subdivision of 1985 survey into strata (stratum 1 is the spawning area; stratum 0 is devoid of eggs).

The egg mortality model

$$P_{ijt} = P_i e^{-Zt} \qquad (3)$$

was fit to the data by a weighted nonlinear least-squares regression, with station-weighting factors used as the weights,

where P_{ijt} = the number of eggs of age t from the j^{th} station in the i^{th} stratum,
t = the age in days measured as the elapsed time from the time of spawning to the time of sampling at the j^{th} station (because spawning occurs once a day and because the incubation period was 3 days or less, as many as 3 cohorts of eggs could be found at each station),
Z = the instantaneous rate of mortality on a daily basis,
P_0 = the daily egg production rate in stratum 0; it is zero by definition, and

P_1 = the daily egg production rate in stratum 1.

Mean half-day frequencies for the age data along with the fitted curve and a 95% confidence region for the regression line are described in Figure 5. By definition, the number of eggs produced in stratum 0 is zero. The daily egg production rate for the total survey area and its variance (Jessen 1978) is:

$$P = (A_1/A)\,P_1 \tag{4}$$

$$\mathrm{var}(P) = (1 + 1/n)[(A_1/A)\,\mathrm{var}(P_1)] \tag{5}$$

where n = the total number of stations,
A_1 = the area of stratum 1, and
A = the total survey area.

The estimates used to compute P, and their variances are given in Table 1. P was found to be 6.41 within stratum 1. For the entire 51,720 n.mi.^{2} survey area, the estimate of P is 4.78 eggs per day per 0.05 m^2 with an approximate variance of 0.33. This gives a coefficient of variation of 12.0%

ADULT PARAMETERS *W*, *F*, *S*, AND *R*

The parameters W, F, S, and R were estimated from a sample of adult anchovies collected by midwater trawl. For each parameter (here denoted y), a weighted mean, $\bar{\bar{y}}$, and a weighted variance were estimated (Cochran 1963):

$$\bar{\bar{y}} = \sum_i [(m_i/\bar{m})\bar{y}_i]/n \tag{6}$$

$$\mathrm{var}(\bar{\bar{y}}) = \sum_i [(m_i/\bar{m})^2(\bar{y}_i-\bar{\bar{y}})^2]/[n(n-1)] \tag{7}$$

where m_i = the number of fish subsampled from the i^{th} trawl,
$\bar{m}$ = the average number of fish subsampled per trawl,
n = the number of positive trawls,
$\bar{y}_i$ = the average value for the i^{th} trawl = $\sum_j y_{ij}/m_i$, and
y_{ij} = the observed value for the j^{th} fish in the i^{th} trawl.

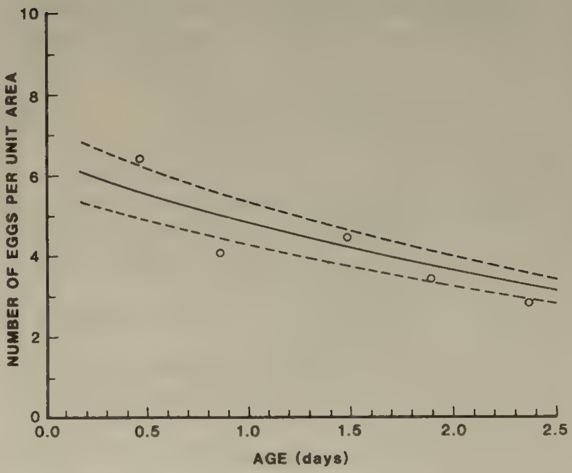

Figure 5. Egg mortality curve. The data are summarized as the mean abundance by half-day intervals, although the regression was fit to the individual data points. A 95% confidence region for the regression (*broken lines*) is indicated.

Average Female Weight

The average weight of an adult female, W, and its variance were estimated using equations 6 and 7, where $\bar{y}_i$ was the average female weight in the i^{th} trawl. I computed average female weight by selecting 25 mature females from each trawl; however, this was not always possible because some trawl samples were too small or were dominated by immature fish.

Just prior to spawning, the eggs in a mature female's ovaries become bloated with fluid (hydrated). I corrected for the extra weight of the hydrated eggs by regressing the weight of mature females without hydrated eggs against their ovary-free weight and then estimating the weight of the hydrated females as if they

TABLE 1
Parameters for Computing Daily Egg Production

	Stratum 0	Stratum 1	Total survey
P (eggs/day-0.05m^2)	0	6.41	4.77
var(P)	0	0.44	0.33
Z (day^{-1})	0	0.29	0.29
var(Z)	0	0.007	0.007
A (0.05m^2)	0.904×10^{12}	2.644×10^{12}	3.548×10^{12}
PA (eggs/day)			16.95×10^{12}
var(P)			4.11×10^{24}

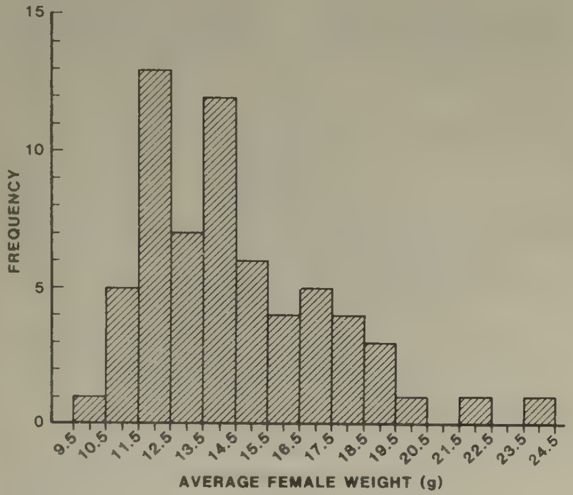

Figure 6. Frequency distribution of average mature female weight per trawl.

did not contain hydrated eggs. The following regression equation was found:

$$\hat{W} = -0.3030 + 1.09\,W^* \qquad (8)$$

where $\hat{W}$ = estimated weight in grams, and
W^* = ovary-free weight in grams.

The regression was highly significant, with a significance level much less than 0.001. The frequency distribution for average weight per trawl is described in Figure 6. The average weight of a female for the entire survey, W, and its variance are listed in Table 2.

Batch Fecundity

The batch fecundity, F, for each mature female is the average number of eggs spawned per female at each spawning event. The batch fecundity was estimated for each female fish by a two-step process. The first step was a regression of batch fecundity versus ovary-free weight from a sample of 85 hydrated females (Figure 7). The ovary-free weight distribution of these 85 fish was similar to the ovary-free weight distribution of all mature females (Figure 8). The estimated regression equation was:

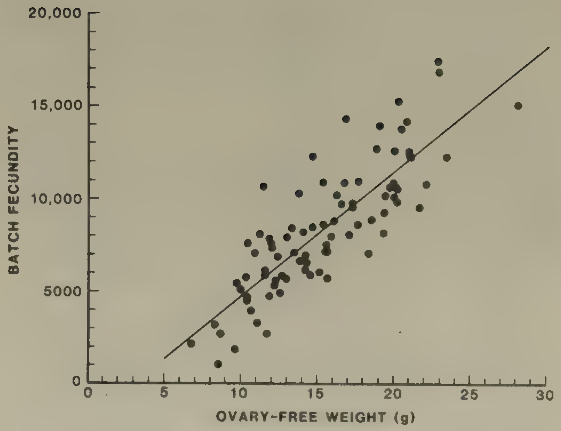

Figure 7. Linear regression of batch fecundity on ovary-free weight fit to 85 females with hydrated ovaries.

$$\hat{F} = -2035.6 + 682.1\,W^* \qquad (9)$$

where $\hat{F}$ = the estimated fecundity for a female with W^* ovary-free weight. The regression was highly significant, with a significance level less than 0.001. The second step was to estimate the batch fecundity for each mature female fish from its ovary-free weight and the above regression. I estimated the average batch fecundity for the entire survey area by using equation 6 where $y_{ij} = \hat{F}_{ij}$, the estimated batch fecundity; the de-

TABLE 2
Estimates of Egg Production Parameters, Variances, and Coefficients of Variation

Parameter		Value	Variance	Coefficient of variation
Daily egg production (eggs/day)	(PA)	16.95×10^{12}	4.11×10^{24}	15.6%
Average female weight (g)	(W)	14.494	0.105	2.2
Batch fecundity (eggs)	(F)	7,343.	1.145×10^{5}	4.6
Spawning fraction (day^{-1})	(S)	0.120	0.00024	12.9
Female fraction	(R)	0.610	0.00038	3.2
Daily specific fecundity (10^6 eggs/day -MT)		37.003		
Spawning biomass (MT) (not including San Francisco area)	(B)	458,024	7.374×10^{9}	18.7
Spawning biomass (MT) (including San Francisco area)	(B)	522,000		

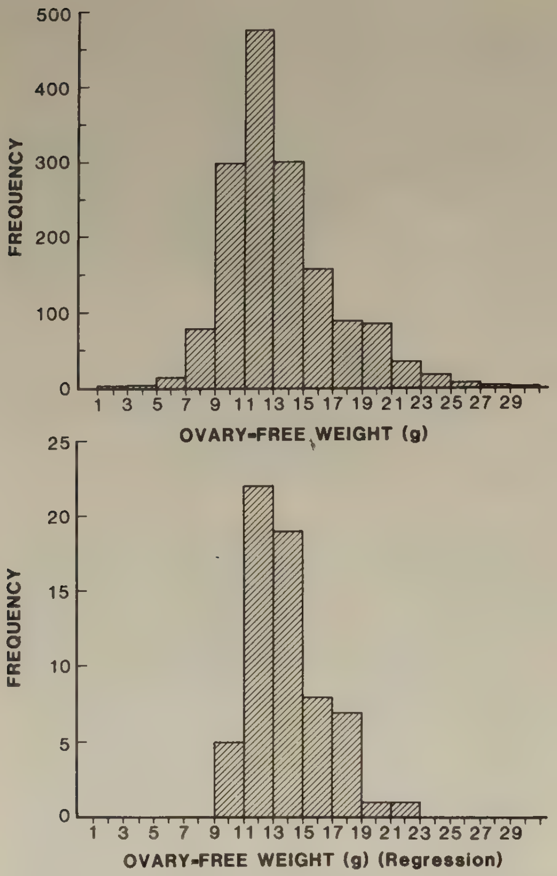

Figure 8. Frequency distributions of ovary-free weight for the entire survey (*top*) and for the females with hydrated ovaries used to estimate the batch fecundity/ovary-free weight regression.

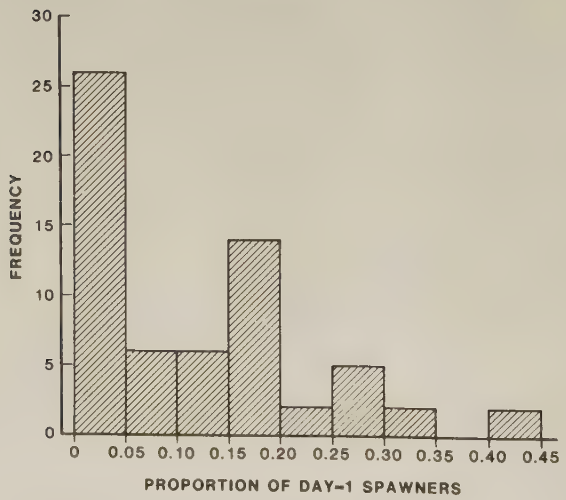

Figure 9. Frequency distribution of spawning fraction.

sired m_i was 25 females. The variance equation (7) was modified because of the extra source of variation from the fecundity/ovary-free weight regression (Draper and Smith 1966):

$$\mathrm{var}(\bar{\bar{F}}) = \sum_i (m_i/\bar{m})^2[(F_i - \bar{F})^2/(n-1) + S_h^2/85 + (\bar{W}_i^* - \bar{W}_h^*)^2 \hat{\mathrm{var}}(b)]/n \qquad (10)$$

where S_h^2 = 3,748,191 is the variance about the regression,
$\bar{W}_i^*$ = average ovary-free weight for the i^{th} trawl,
$\bar{W}_h^*$ = 15.43 g, average ovary-free weight of the 85 hydrated females used in the regression,
vâr (b) = 2,453, variance of the slope of the regression, and
n = 63, the number of positive trawls.

The average batch fecundity and its variance appear in Table 2.

Spawning Fraction

The spawning fraction is the proportion of mature females that spawned on the night prior to capture (day-1 spawners). The spawning fraction, S, and its variance were estimated using equations 6 and 7 where $\bar{y}_i = S_i$ was the spawning fraction found from the i^{th} trawl. The desired m_i—the sample size per trawl—was 25. Strong evidence indicates that females spawning on the night of capture (day-0 spawners) are oversampled by the trawl (Picquelle and Hewitt 1983). To account for this, I adjusted m_i by assuming that there was an equal incidence of day-0 and day-1 spawning fish and hence substituting the day-1 spawners for the day-0 spawners. The frequency distribution of the spawning fraction appears in Figure 9. The estimate of S and its variance are found in Table 2.

Female Fraction

The female fraction of the population by weight is the parameter R. Equations 6 and 7 were used where $\bar{y}_i = R_i$, the total weight of females in a subsample of approximately 50 fish divided by the total fish weight. For each trawl, average weights of male (n = 5) and female (n = 25) fish were measured, and the weights of hydrated females were adjusted using the regression given in equation 8. These average weights were used to estimate the total female weight and the total fish weight. The frequency distribution of R is given in Figure 10; the estimate and variance are shown in Table 2.

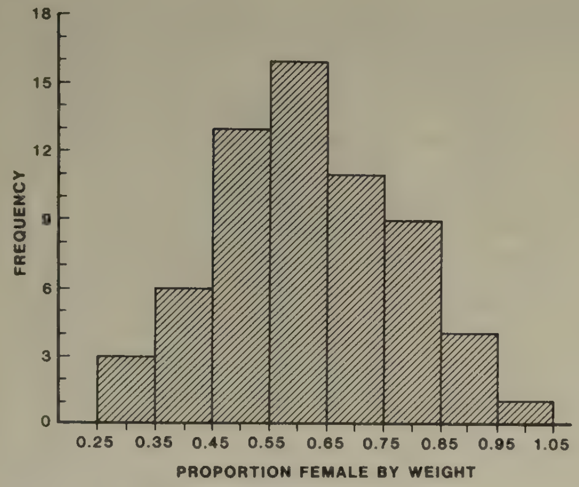

Figure 10. Frequency distribution of female fraction by weight.

BIOMASS ESTIMATE AND VARIANCE

Using equations 1 and 2, I estimated the spawning biomass for the portion of the population range covered by the survey to be 458,025 MT, with a standard error of 85,872 MT. This gives a coefficient of variation of 18.75% The values of the parameters that were used in the estimate, and their variances and covariances appear in Tables 2 and 3. The northern part of the population range was not covered by this survey.

The results of the *Mys Babushkina* cruise show that, as in past years, there is spawning off San Francisco. The Soviet cruise covered the area from Point Conception (CalCOFI line 80.0) north to line 70.7—the northern extent of our biomass survey (region 2)—as well as the region north of line 70.7 (region 1). The Soviets used a bongo net to collect anchovy eggs and larvae. Because larvae are less patchy than eggs, I used "scanned" larvae counts (Figure 3) as an indicator of relative spawning biomass in the two regions. Specific fecundity and subsequent mortality rates of eggs and larvae are assumed to be constant throughout the spawning area. The biomass of region 1 was calculated as:

$$B1 = B2 * \frac{\sum_{i} (L1_i * A_i)}{\sum_{i} (L2_i * A_i)} = 63{,}718 \text{ MT}$$

where $B1$ = estimated spawning biomass of region 1,

$B2$ = 29,090 MT is the spawning biomass of region 2 (biomass equation),

$L1_i$ = number of larvae caught at each station in region 1,

$L2_i$ = number of larvae caught at each station in region 2, and

A_i = area represented by station i.

The final biomass estimate for the survey area plus the northern area was 458,025 + 63,718 = 521,742 MT. The variance of this estimate was not computed. However, the coefficient of variation is certainly larger than the 19% associated with the entire region of the EPM survey (Table 2).

DISCUSSION

The 1985 egg production method estimate of the spawning biomass of the central subpopulation of the northern anchovy is up by 61% from its lowest point (since 1980) in 1984. Table 4 lists the historical time series of parameters. The change in spawning biomass is caused by a 31% increase in egg production and a 13% increase in the daily specific fecundity from 1984. The decrease in daily specific fecundity results from a drop in the spawning fraction to a level average for 1980-84 and an increase in batch fecundity. The larger batch fecundity is strongly related to a 21% increase in female weight, because the two are highly correlated (Table 3). The ratio of batch fecundity and mean weight (F/W) estimates the specific batch fecundity (Table 4). The increase in this ratio is less than the rise in batch fecundity, implying that much of the growth in batch fecundity is due to a larger average female weight. The egg mortality rate Z was higher this year than it has been since 1980. The very large 1980 rate, along with this year's high Z value, demonstrates the variability of Z. Female fraction remained very high compared to the years before 1984. The daily specific fecundity is lower than 1984 but is still above the average for 1980-83.

The EPM spawning biomass estimate can be compared to an annual acoustic survey, which provided a measure of total anchovy biomass. The California Department of Fish and Game conducted an acoustic and midwater trawl survey of the northern anchovy in February 1985 (Cruise Report 85-X-1, K.F. Mais, CDFG, Long Beach, California). The cruise was restricted to the area between Point Conception (CalCOFI line 80.0) and the U.S.-Mexican fishery boundary. In agreement with our results, Mais reports that the geographic distribution of anchovies was more offshore

TABLE 3
Covariances between Adult Parameters

	F	S	Female fraction (R)
Female weight (W)	66.25495	0.00076	0.00064759
Batch fecundity (F)		0.53235	0.44352668
Spawning fraction (S)			0.00005531

TABLE 4
Time Series of Egg Production Parameters (1980-85)

		1980	1981	1982	1983	1984	1985[a]
Daily egg production (10^{12} eggs/day)	(*PA*)	26.34	20.96	13.51	17.25	12.98	16.95
Egg mortality rate	(*Z*)	0.45	0.14	0.16	0.18	0.17	0.29
Average female weight (g)	(*W*)	17.44	13.37	18.83	11.20	12.02	14.50
Batch fecundity (eggs)	(*F*)	7,751	8,329	10,845	5,297	5,485	7,343
Spawning fraction	(*S*)	0.142	0.106	0.120	0.094	0.160	0.120
Female fraction	(*R*)	0.478	0.501	0.472	0.549	0.582	0.609
Daily specific fecundity (10^6 eggs/day/MT)		30.28	33.03	32.53	24.35	42.43	37.00
Specific batch fecundity (eggs/g)	(*F/W*)	444	623	576	473	456	506
Spawning biomass (10^3 MT)	(*B*)	870	635	415	652	309	522[b]
Coef. of variation for (*B*)		0.26	0.22	0.06	0.21	0.17	0.19[a]
Calif. Dept. Fish and Game acoustic biomass estimate (10^3 MT)		498 to 598	493 to 591	233 to 247	461 to 504	479 to 560	627 to 753[c]

[a] Does not include San Francisco area
[b] Includes San Francisco
[c] Does not include Mexican portion of anchovy population

and southward than in any other survey year. He also reported that the bulk of the population was "located in an arc of 80 miles west to south, and 30 miles east to south of San Clemente Island." This is where our survey found the greatest density of anchovy eggs (Figure 1). Mais calculated the total biomass of anchovies (not spawning biomass) to be 627,000-753,000 MT in U.S. waters off southern California. This is up 30.8%-34.5% from his results of 1984. He concludes that the 1985 estimate is the highest in five years and that it would have been higher if the proportion of the anchovy population located in Mexican waters been included.

In previous years the survey area was divided into regions in order to reduce the variance of the parameters and the variance of the biomass estimate (Picquelle and Hewitt 1983; Hewitt 1984). The regionalization was indicated because there were significant differences in one or more parameters between regions. There is no indication that regionalization would have reduced the variance of this year's estimates.

Anchovy eggs were found much farther offshore than in any year since the egg production method surveys began in 1980. A large number of eggs far offshore may have been missed by our survey. As mentioned earlier, if a significant number were missed, there would be a downward bias in our biomass estimate.

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AN APPROACH TO RECRUITMENT RESEARCH IN INSULAR ECOSYSTEMS

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ABSTRACT: Population maintenance of species with pelagic larvae in island systems is poorly understood, but general agreement has emerged in recent years that processes in the plankton are responsible for recruitment variability. An initial, multi-disciplinary approach is suggested to examine questions of population maintenance with special attention to retention of larval forms around islands. Intensive but directed studies of physical and biological oceanography in waters surrounding an island and studies of fish populations, including recruitment patterns on the island, are proposed. A rationale is developed for the initial study to be conducted at an isolated, oceanic island to simplify the survey work and interpretation of results. Such a study could lead to new insights on the planktonic processes which affect recruitment variablity and would be invaluable to the design of similar studies in more complicated archipelagic or tropical coastal systems.

1. INTRODUCTION

Marine organisms which inhabit isolated islands or seamounts are faced with limited adult habitat and with ocean currents which advect larvae away from the source population; some species have probably developed mechanisms for population maintenance, but these remain largely unknown at the present time. Thus the problems of recruitment of island and seamount resources differ significantly from those of species associated with continental shelf and slope regions, regardless if in boreal, temperate, or tropical regions. In this paper I consider some of the questions which must be addressed if we are to better understand the process of recruitment in island and seamount ecosystems.

The vast majority of tropical marine species, particularly those of commercial importance, are characterized by a life history with a pelagic larval stage. While early studies typically suggested that these stages were adaptive for dispersal (Ekman,1953), an alternate view was developed by Johannes (1978), who argued that pelagic larvae were an adaptation to minimize predation of the vulnerable larval stages. Still, other scientists hold to the concept that dispersal remains the selective advantage of a pelagic stage (Barlow, 1981).

To understand recruitment in insular ecosystems, the above issue is important but the fact remains that pelagic larvae must return to replenish the source population. Several early studies of reef fish ecology held that space, rather than recruitment, was the limiting factor to these populations (Smith and Tyler 1972, 1975), inferring that a large pool of potential recruits could fill space on the reef at any time. If this were indeed the case, fishery exploitation of a given population size could possibly be maintained at a higher level than if recruitment were variable and the limiting factor. Unfortunately, more detailed study has shown that recruitment is highly variable within species. On a short time scale, Victor (1982) has shown sporadic recruitment despite continuous spawning in the labrid _Thalassoma bifasciatum_. Other studies have further demonstrated that recruitment is one of the most important factors in the population dynamics of reef fishes (Doherty, 1983; Williams, 1983; Sale and Douglas 1984). The temporal component of recruitment variability is probably the most important, with interannual differences of at least an order of magnitude (Shulman 1985). Spatial variations, at least on the scales examined, would appear to be less important. Similar recruitment patterns may occur over scales of 1 km (Shulman, 1985) to 50 km, the latter apparently after mixing of cohorts in the plankton (Victor, 1984). Eckert (1984), however, noted little similarity in spatial recruitment patterns in a series of reefs in the Great Barrier Reef system, and Sale _et al_. (1984) suggested that spatial variability on this scale is as important as variability in year class strength. The question of spatial variations and its relationship with temporal variability needs more work.

Since the source of variability in recruitment occurs in the planktonic stage (Victor,1983; Warner,1984) this is an important place to begin investigations. The important processes to address initially must be whether variability in recruitment is under physical or biotic control. If the pelagic larval stage is an adaptation to reduce predation as suggested by Johannes (1978), then biotic effects in the planktonic environment may not result in a strong component of interannual variability. Planktonic prey of fish larvae may be enhanced on the mesoscale by the "island mass effect" (Gilmartin and Relevante,1974) and the associated higher standing stocks of plankton near islands (Jones,1962). Physical factors, on the other hand, may play a more important role in recruitment variability. Physical oceanography around islands is complex and variable (Barkley,1972; Hogg et al.,1978; Pingree and Maddock,1980, 1985) and advection likely plays the dominant role in variability in recruitment strength in tropical island species. In the life history, biotic factors may play the dominant role after settlement.

2. MECHANISMS OF POPULATION MAINTENANCE

The physical mechanisms important in larval retention around islands, banks, or seamounts have been discussed by Bakun (this volume) and I will not elaborate on them here. The physical processes alone, however, are not likely to result in retention of larvae; related biological processes, such as temporal spawning activity by adults and behavioral attributes of the planktonic stages, doubtless interact with the physical mechanisms to result in retention and ultimate recruitment (Lobel and Robinson,1983). While flow patterns may result in significant aggregation of planktonic organisms under certain situations (Hamner and Hauri, 1981), insular holoplanktonic assemblages distinct from oceanic assemblages occur around islands and patterns of convergences may maintain such populations (Boden,1952). Peterson et al. (1979) described a similar mechanism for maintenance of a copepod population in an upwelling area, but invoked a behavioral mechanism to explain differential utilization of current patterns. Larvae are capable of significant behavioral responses to physical factors which may result in alterations in the distribution pattern (Boehlert and Mundy, 1986).

Eddies and gyres which form around islands and seamounts may act to trap waters for significant periods of time (Pingree and Maddock,1980; Wolanski et al. 1984). Sale (1970), Emery (1972), and Shomura and Barkley (1979) suggested that such eddies were important in retaining planktonic stages. Further conceptual development of this idea has been provided by Lobel and Robinson (1983); data supporting the role of eddies in population maintenance exist for the continental shelf off Norway (Sundby,1984), Rockall Bank (Dooley,1984), and George's Bank (Smith and Morse,1985). Understanding the physical and temporal attributes of such eddies will be necessary to show their importance in a recruitment mechanism.

3. CURRENT RESEARCH APPROACHES

The study of recruitment has historically taken indirect approaches which look at the final result, including age distributions, year class strengths, and, in the case of reef fishes, temporal and spatial recruitment patterns, looking at the results of the process of recruitment rather than the mechanism. Many of the recent studies outlined above demonstrate significant temporal variability in recruitment, including interannual variability, despite a relatively stable spawning stock. The work of Victor (1983, 1984), in particular, points to processes in the plankton which determine the timing and strength of recruitment in tropical systems (Warner, 1984). The northern anchovy in the California Current system was studied for many years as part of the CalCOFI program and this historical data base on larval distribution and abundance has been critical to further work; the greatest advances in understanding causes of recruitment success or failure, however, have been made in the last decade by determining the role of physical (storms, turbulence) and biotic (prey microdistribution) factors (Lasker 1975, 1978) and their effects on mortality in the field. This approach has allowed generalities to be drawn about similar ecosystems (Bakun, 1985). A comparative approach could also be profitable in tropical systems.

Much of the research on recruitment in tropical fishes has addressed the issue of the high diversity of reef fishes (Sale, 1982), but recent studies on recruitment have directed more researchers to look to processes in the plankton as determinants of recruitment (Helfman, 1978; Doherty et al. 1985; McFarland and Ogden, 1985). Studies on the reef have documented spawning activity and recruitment patterns, but little research has been done on the intervening pelagic stage (McFarland and Ogden, 1985). Still, research on the growth patterns of recruits has resulted in a greater understanding of the timing and variability of recruitment. Use of daily growth increments on new recruits and the ability to detect "recruitment marks" on older ones (Ralston, 1975; Brothers and McFarland 1979) has led to inferences regarding age at recruitment for many species (Brothers and Thresher, 1985; Brothers et al. 1983). Application of this technique to a single species has shown a high degree of spatial coherence in recruitment pattern over a scale of 50 km in the Caribbean (Victor, 1984); this study was significant in that the ages within groups recruiting at the same time were mixed, suggesting that cohorts spawned at different times were mixed in the plankton. These studies are important and allow us to draw inferences about processes occurring in the planktonic environment.

There have been fewer studies in the pelagic environment in tropical ecosystems which relate to recruitment. Distributional studies have typically lacked the detailed physical measurements necessary to understand the meaning of observed patterns. Several intriguing results nonetheless exist. Miller (1974), for example, noted differences in abundance of fish larvae upstream, downstream, and in the reef waters of Molokini, a small islet near Maui in Hawaii; larval fish in reef waters and downstream were typically smaller than in upstream waters, but were 26 and 4 times as abundant, respectively. It is known that areas of stagnant water may be held in the lee of islands in response to a current (Pingree and Maddock, 1980; Wolanski et al. 1984) and that zooplankton may swarm or form aggregations in such locations (Hamner and Hauri, 1981). An interesting point of Miller's study, however, was that densities of passively transported tunicate eggs did not differ among the three areas, suggesting that larval behavior was an important feature of the observed distributional patterns. Other studies in Hawaii have documented differences in distributional patterns among different groups of ichthyoplankton (Leis and Miller, 1976; Leis 1982b); Leis (1982a) has also used eggs and larvae of nearshore species as tracers of coastal water but later suggested that "the assumption that larvae of reef fishes are passive particles to be treated as conservative properties of water parcels is unjustified without much more information than is currently available on larval behavior" (Leis and Goldman,1984). While these studies provide intriguing results, they lack the concurrent physical data necessary for firm interpretation. More recent studies on small reefs within the Great Barrier Reef have included physical measurements (Leis and Goldman,1983, 1984; Williams et al. 1984).

4. AN APPROACH TO UNDERSTANDING INSULAR RECRUITMENT MECHANISMS

Components of a fairly comprehensive program addressing insular recruitment in the Caribbean were discussed in Richards (1982) and included studies of physical oceanography, larval distribution, planktology, primary productivity, and fisheries data analysis. In this paper I recommend a more modest approach for an initial but intensive study. If we agree that processes in the plankton are the major source of variability in recruitment, then we narrow the primary sources of this variability to either physical (advection) or biotic (predation, prey availability) factors (Hunter,1976). While the biotic factors doubtless play a role, study of predation- or starvation-induced mortalities may be premature in tropical ecosystems, mainly because our understanding of distributional patterns is somewhat rudimentary and abundances of shore-fish larvae are quite low (Leis and Miller,1976). Reef fishes typically have extended spawning seasons and apparently use a planktonic stage to reduce predation on the reef (Johannes,1978; Thresher and Brothers,1985); also, species with planktonic eggs may spawn in a manner which minimizes temporal and spatial overlap with predators (Frank and Leggett,1985). Although predation may be an important source of interannual variability in mortality of larval stages, it will be difficult to study without knowledge of distribution. Advection and other physical factors may initially be a more tractable problem for study and clearly play an important role in recruitment variability in tropical island ecosystems. While not intensively studying prey and predator distribution, an initial study of advection, distribution, and retention mechanisms would provide preliminary distributional data which could later be used to design studies of prey microscale distribution (Owen,1981) or predation and starvation (Hewitt et al. 1985).

Another way to simplify an initial tropical recruitment experiment would be to conduct the work around an isolated, oceanic island. This provides two advantages. First, the complexities in physical oceanography inherent in archipelagic systems, including eddies and downstream effects, will be minimized (Barkley,1972). Secondly, it avoids the problem of an unknown source population. Early larvae and the vast majority of recruits of shore fishes captured near an isolated oceanic island were likely spawned there. Shore-based studies of recruitment (Victor,1982, 1984; McFarland et al. 1985; Shulman,1985) have typically not addressed the problem of the source of recruits. With a pelagic duration of 20-50 days (Brothers and Thresher,1985), recruits could come from a wide geographic area. Remaining in an isolated system for an initial experiment thus has the advantage of providing a better understanding of the primary mechanisms involved in larval retention and recruitment which may then be applied to more complicated systems; it also will address the question of locally recruiting populations proposed by Bakun (this volume). Another advantage is that the populations may be unexploited and thus population characteristics such as age distribution and natural mortality can be determined from sampling and age analysis.

The proposed study would involve physical and biological components. The physical oceanographic component would involve primarily measurements of mesoscale phenomena, first looking at the general geostrophic flow component and its variability and studying the effects of the island on flow, including both local and downstream effects. Specifically, the physical retention mechanisms considered in Bakun (this volume) must be evaluated to assess their ability to retain larvae and juveniles in the region of the island. In the initial, intensive studies, special consideration should be given to developing simpler means of determining flow patterns, including use of XBT data, perhaps in conjunction with objective analysis models (Mooers and Robinson, 1984), should they prove reliable in waters around islands. Special attention should also be paid to remote sensing methods. Surface thermal images in the tropics may not be of great value, but ocean color analysis can be used to detect variations in chlorophyll which might be related to island effects (Dandonneau and Charpy, 1985). Similarly, satellite altimetry could potentially be used for detection of eddies or current patterns and may facilitate subsequent detection of the appropriate signals.

The biological program in offshore waters will be primarily shipboard sampling and should concentrate on local island species. Sampling for variability in abundance and microdistribution of prey, primary productivity, and other trophic factors would be minimized in this initial study. Patterns of chlorophyll distribution, however, should be taken to ground-truth remote sensing proposed for the physical component. Initially, a large scale spatial study of larval and juvenile fish distribution will be necessary, including upstream/downstream sampling and intensive sampling in the island wake region and nearshore waters. As an example, preliminary data on horizontal ichthyoplankton abundance around Johnston Island (Figure 1) demonstrate that larval abundance in downstream waters may be several times higher than in upstream waters; the increases are explained by increases of shore-fish larvae as opposed to midwater or noninsular forms. Unfortunately, concurrent physical data are unavailable from this study to test the retention mechanisms proposed by Bakun (this volume). Limited sampling should also be conducted in the shallows or lagoon waters, but these have not typically been shown to be important nurseries for most species (Leis, 1981; Leis and Goldman 1983). The ichthyoplankton sampling should be conducted with high resolution in the vertical plane, with concurrent sampling of physical factors (depth, temperature, salinity) as is done with the MOCNESS or BIONESS nets. Scoping studies should be done to determine the depths of residence of shore fish larvae and these depths should be studied intensively to minimize the needed sampling; typically, the upper mixed layer is where the majority of shore fish larvae will be found in tropical systems, as shown for waters off Hawaii (Figure 2). Studies of the relationship of larval distribution to physical and diel factors can then be used to infer behavioral patterns and their role in the physical retention mechanisms.

Larger volume sampling techniques, particularly midwater trawls, should be used to define the horizontal patterns of larger larvae and transformed juveniles which are rare or undersampled by the plankton gear; to maximize the use of shiptime, large nets as described in Pearcy (1980) which are semi-quantitative and have uniform mesh, should be used. Such large sampling gear was used by Sale (1970), who observed overall densities of juvenile convict surgeonfish, Acanthurus triostegus, of 0.0017 per 1000 m^3. Although these densities are low, such nets may sample 100 m^3 per second when towed at 2 kt and thus detect areas of moderate density with reasonable sampling times.

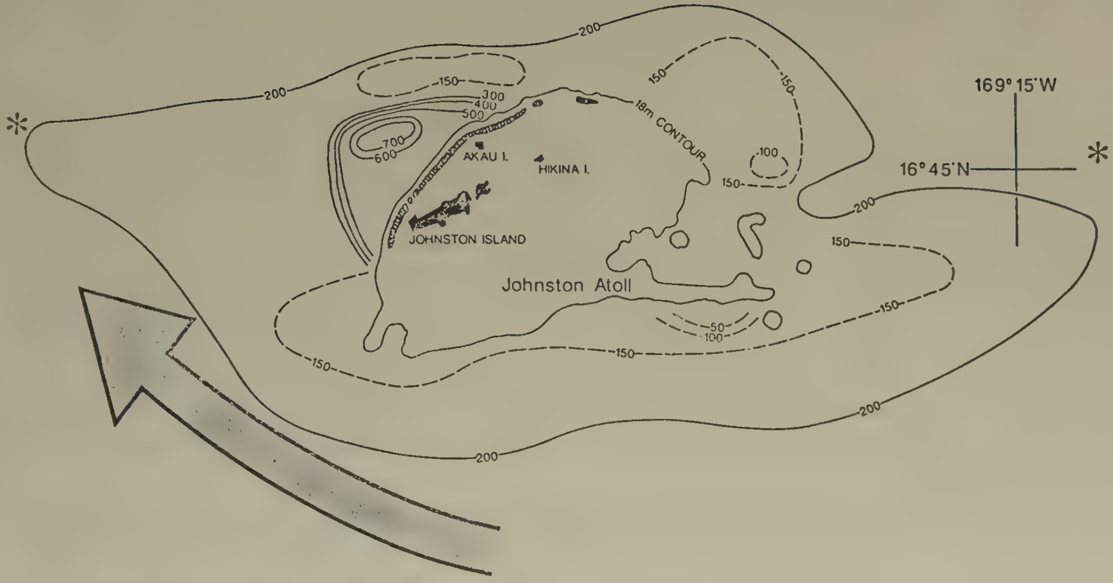

FIGURE 1. Distribution of ichthyoplankton around Johnston Island in November, 1984 collected from the Townsend Cromwell with a 1 m^2 opening-closing Tucker trawl. Densities refer to numbers of larvae per 10^3 m^3 in the 50-100 m depth stratum. The arrow represents surface current deduced from drogues deployed a month earlier (P. S. Lobel, personal communication). Note the high density of larvae on the downstream side of the island. Data from Boehlert (unpublished). Asterisks indicate that collections were made at greater distances east and west of the atoll.

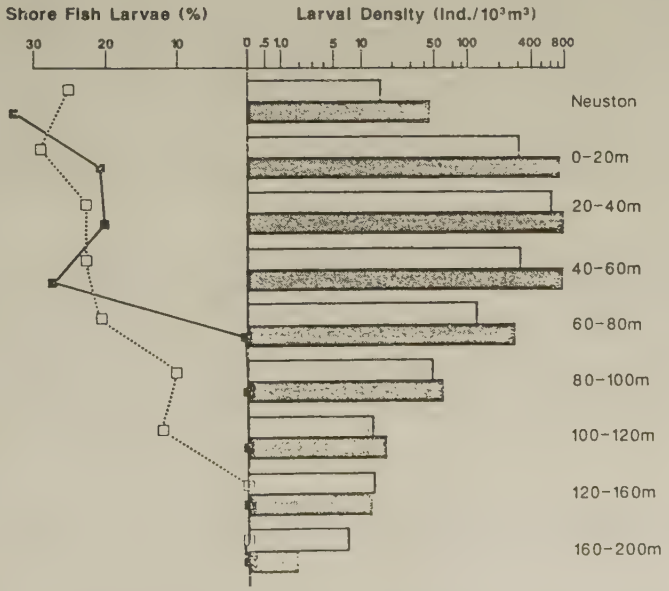

FIGURE 2. Larval densities (log scale) as a function of depth at both day and night at a station 5 nmi off the leeward coast of Oahu, Hawaii (lat. 21°21' N., long. 158°13.3' W.) taken in September, 1985. Each value represents a single haul. Clear bars represent day densities, cross-hatched bars represent night densities. The neuston samples are from the surface to 70 cm. On the left of the figure, the percentage of shore fish larvae (as opposed to pelagic or midwater fishes) is shown, with closed squares representing night, open squares day samples. Data from Boehlert and Mundy (unpublished).

A nearshore biological component of this study should be developed to sample all life stages from new recruits to adults. The age structure of adult populations should be determined with sufficient numbers to allow both estimation of mortality rates and variability in year class strength. These should be combined with length-based methodologies to streamline subsequent sampling. Sampling of new recruits should be undertaken during and after the main offshore sampling. This part of the study should at least include surveys to assess the densities of recruits and otolith studies to determine the birthdate and settlement date distribution of recruits. This will provide both the planktonic duration and the success of cohorts sampled during earlier offshore work. The latter work would be particularly important to correlate with physical oceanography and the distribution and abundance of earlier life stages in the pelagic environment.

From a temporal standpoint, the intensive study should be conducted during the season which coincides with the spawning peaks of most reef species, but preferably for a longer period in the first year to assess seasonal variability. The duration of the intensive offshore study should be at least one month, which will allow the distributional and physical analysis as well as coinciding with the approximate pelagic duration of many fish species (Brothers and Thresher, 1985). This type of study should be conducted over a period of two or three years (with more precise and therefore less intensive sampling each year) to assess interannual variability. If remote sensing methods prove useful, relevant data could be collected throughout the year.

This study should concentrate on any insular species to allow flexibility. Target species attributes should include known life histories (identified larvae, juvenile stages and habitats), sufficient larval and juvenile abundance to statistically assess distributional patterns and recruitment, and a large enough adult population to allow repeated sampling and estimation of population age structure. As with any ichthyoplankton program, however, the proposed research should consider the suite of species captured in the study to evaluate species associations.

If framed as a two to three year study, this research could provide answers to many unanswered questions about recruitment in tropical insular ecosystems. The study of an isolated island ecosystem would provide focused hypotheses which could then be tested in the more complicated archipelagic and island group systems where fisheries for a variety of species with pelagic eggs and larvae exist. To achieve these objectives, however, an intensive and interdisciplinary approach will be necessary.

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Productivity and Population Maintenance of Seamount Resources and Future Research Directions

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ABSTRACT

Seamounts represent ocean features whose potential for biological resources has been largely overlooked. The recent discovery of abundant fish resources in the southern Emperor Seamounts region, however, has led to fisheries development and exploitation. We have little understanding of basic biological and population characteristics such as recruitment patterns, age distribution, the stock-recruit relationship, natural mortality, and trophic relationships among seamount species to form the basis for appropriate management. Seamount fisheries differ in many respects from other fisheries so that innovative methods are needed to evaluate resource characteristics. Available information suggests that interaction of seamounts with ocean currents results in flow complexities including Taylor columns and eddies which may either increase productivity or aggregate prey organisms. Thus, seamounts may play important roles in the concentration of biological resources. Understanding the productivity and sustainability of these resources requires multidisciplinary approaches involving physical and biological oceanographic research.

INTRODUCTION

Seamounts are a dominant feature of the geomorphology of the Pacific Ocean, yet they have received relatively little study. Logistic constraints have generally limited biological investigations to small-scale efforts designed to consider the fauna present in particular locations (Pratt 1967; Raymore 1982). In the northern and central Pacific, however, the discovery of exploitable biological resources has intensified the study of the value and sustainability of seamount fishery resources in the Gulf of Alaska (Hughes 1981) and in the southern Emperor-northern Hawaiian Ridge (SE-NHR) region (Humphreys et al. 1984). Seamounts in the Gulf of Alaska have fish populations similar to those in coastal waters but unexpectedly high densities of several species of crabs (Hughes 1981), but no directed fishery has developed to exploit these resources. In the SE-NHR seamount group (Fig. 1) the development of a fishery preceded fisheries research. Since that time, new fisheries have developed, including those for bottom fishes besides pelagic armorhead, *Pseudopentaceros wheeleri* (Humphreys et al. 1984), precious corals (Grigg 1982), albacore (Yasui 1986), skipjack tuna (Inoue 1983), and squid.

Traditional fisheries research is difficult to conduct on seamounts. Seamounts are generally remote, making seasonal, repeated sampling difficult. Often, the fine-scale topography of the shallow portions of the seamounts is poorly known, although bathymetric studies continue (Smoot 1985). In the SE-NHR seamounts relatively little is known about the life history and ecology of the dominant species, their habitats, and the associated ecosystem; thus new approaches will be necessary to assess and determine the sustainability of the resource.

Although limited in area, seamounts may serve as locations for concentration and transfer of energy from the pelagic to demersal ecosystems. Demersal resources of seamounts may maintain high biomasses as a result of localized enhancement or concentration of the productivity of overlying waters. Our understanding of this productivity is largely at the hypothetical stage and few data exist. It is thus difficult to draw conclusions about possible mechanisms that maintain these large demersal populations. If productivity is indeed high, one can understand how large populations of fishes, deriving nutrition from overlying waters, could develop over time. A major concern, however, is the sustainability of these populations. On mid-Pacific seamounts, currently depressed populations of pelagic armorhead may not allow us to estimate the maximum sustainable yield. Recruitment rates and variability, the stock-recruitment relationships, and the basic ecological processes associated with seamount populations are unknown. Further, it is difficult to find other populations with which to make valid comparisons. Fish populations of seamounts are geographically isolated, but no evidence exists to suggest that stocks of dominant species are independent between seamounts. These issues will be important to address as we consider further research on seamount resources. It is the purpose of this paper to discuss hypotheses about the maintenance of seamount populations and to suggest future research.

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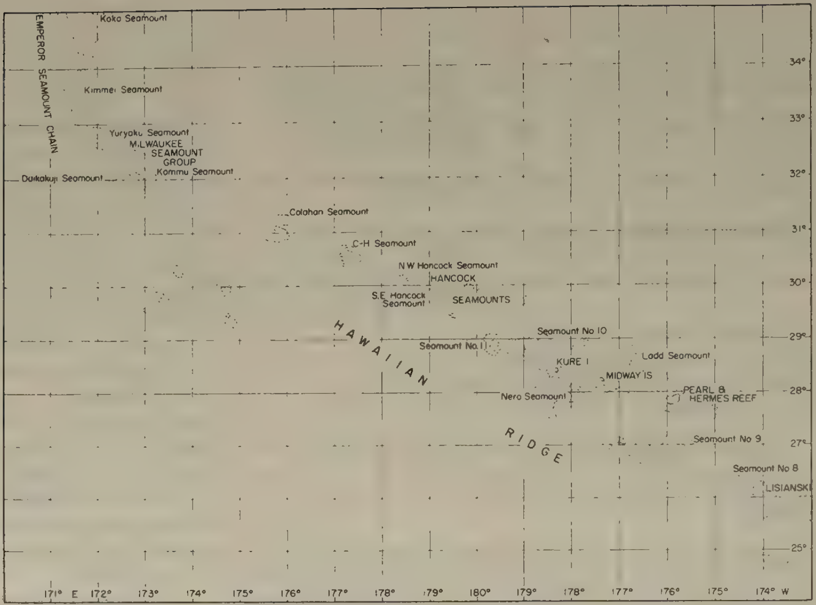

Figure 1.—The southern Emperor-northern Hawaiian Ridge seamounts. The range of the armorhead and alfonsin are largely restricted to the north by the depth of the seamounts and to the south most likely by temperature. Current flow in this region is dominated by easterly flow from the Kuroshio north of the subtropical front, but this front can vary seasonally (and interannually) between lat. 28° and 32°N (Roden 1970); south of the front, westerly flow may be observed.

ENHANCED PRODUCTIVITY OVER SEAMOUNTS

The idea that productivity is enhanced over submarine banks and seamounts is associated with complexities of physical oceanography and is derived, in large part, from the work of Uda and Ishino (1958). They suggested that topographically generated eddies enhance productivity, which is reflected in increased fish catch. In this section I will consider the evidence for increased productivity and the potential for advection and concentration of pelagic productivity from other areas to the seamount regions.

Waters overlying seamounts are often characterized by high standing stocks of plankton (Uda and Ishino 1958; Fedosova 1974; Bezrukov and Natarov 1976). Several ideas exist about the high productivity in the region of seamounts. The effects of seafloor topography on ocean currrents have been reviewed by Hogg (1980). Generally oceanography around seamounts is complicated. Taylor columns, semistationary eddies located above seamounts, have been theoretically predicted for several decades (Taylor 1917; Huppert and Bryan 1976) and actually observed over some seamounts (Owens and Hogg 1980; Richardson 1980). Taylor columns may also be generated over the SE-NHR seamounts, where eddies have been observed (Bezrukov and Natarov 1976; Cheney et al. 1980), but most oceanographic surveys sample too large a grid to detect these open-ocean mesoscale phenomena (Roden 1986). Eddies shed downstream of the seamounts, however, are an important source of variability in the oceanography of the North Pacific (Royer 1978).

Taylor columns may be important in maintaining planktonic populations and may indeed produce increased primary and secondary productivity. From a theoretical standpoint, Taylor column formation is a function of current strength, seamount morphology, stratification of the water column, and latitude (Huppert 1975). Anticyclonic flow around the seamount should exist, with cold water at its center; warm water cyclonic eddies would remain in the vicinity of the seamount at low current speeds and are shed downstream at higher current speeds (Owens and Hogg 1980). The upwelled cold water could bring nutrients to the euphotic zone, resulting in increased productivity. The stationary nature of this eddy over the seamount would also decrease the probability of advection of this productivity from the seamount, making it available to seamount populations. Some support for these arguments is provided by a comparison of waters over seamounts with adjacent waters; differences have been noted in chlorophyll content (Genin and Boehlert 1985), plankton biomass (Bezrukov and Natarov 1976), ichthyoplankton (Nellen 1973; Boehlert 1985), and micronekton (Boehlert and Seki 1984). On a small seamount in the Marianas, however, Genin and Boehlert (1985) showed that the phenomenon seemed to be transitory, but dependent upon the oncoming current strength and the morphology of the seamount.

Uda and Ishino (1958) suggested that increased pelagic productivity may enhance productivity on banks and seamounts, and stated "the concentrated areas of food animals including nekton, plankton and benthic fauna are fertilized by upwelling and accumulated or hydrobiologically limited by convergence." Indeed, the densities of pelagic armorhead alone produced catch rates of some 96 metric tons (MT) per trawling hour on Colahan Seamount in 1972 (Humphreys et al. 1984). Estimated standing stock of this species in the SE-NHR seamount region was as high as 396,000 MT in 1969 (Borets 1975; see Table 1). This species, which forms aggregations off the bottom during daytime and feeds on macroplanktonic and micronektonic animals, is considered to be semidemersal at the seamounts. The biomass of prey organisms necessary to support such a large localized predator population must be immense; it is doubtful that the standing stock under average conditions of the North Pacific Ocean could support this biomass of pelagic armorhead. An analogy may be drawn with surface schooling tunas, which apparently depend upon fronts for prey aggregation (Murphy and Shomura 1972).

Table 1.—Catch and effort from the Japanese and Soviet fisheries for armorhead, *Pseudopentaceros wheeleri*, on the SE-NHR seamounts and estimates of boarfish stock size, 1968-75. Data are from Takahashi and Sasaki (1977) for the Japanese data and Borets (1975) for the Soviet data. Soviet catch data have been converted to weight from numbers by assuming a mean weight of 0.5 kg/fish. Note the difference in units of effort between the Japanese and Soviet data.

Indices	1968	1969	1970	1971	1972	1973	1974	1975
Japanese data								
Catch (10^3 MT)	—	3.28	30.0	5.9	29.9	25.0	34.5	19.0
Fishing effort (trawling hours)	—	157	2,807	1,304	496	740	1,583	1,377
Soviet data								
Catch (10^3 MT)	49.5	162.5	145.0	17.0	98.0	170.5	39.5	46.5
Fishing effort (vessel days)	1,069	3,282	3,516	467	1,883	4,044	1,589	2,047
Stock size (10^3 MT)	310.5	396.0	329.5	221.5	364.0	355.5	173.0	160.5
Recruitment (10^3 MT)	180.5	148	77.5	193.5	140	35	51	—

Mechanisms which aggregate food organisms produced elsewhere may also contribute to energy flow on seamounts. Pereyra et al. (1969), for example, observed concentrations of demersal yellowtail rockfish, *Sebastes flavidus*, feeding in areas where midwater organisms were being advected onto the continental shelf. Isaacs and Schwartzlose (1965) observed a similar pattern on an offshore bank and suggested that such fish populations thus may not be limited by local productivity, but rather depend upon oceanic productivity and advection or hydrographic aggregation of prey sources. Midwater fishes and other organisms in scattering layers may reach very high densities during daytime (Backus et al. 1968). Alldredge and Hamner (1980) described a hydrodynamic aggregation of plankton some fortyfold over mean densities in an eddy system near a coastal headland and suggested that it may have important effects upon fish distributions. Similarly, Olson and Backus (1985) provide data and model a concentrating mechanism for midwater fishes at fronts. Interaction of currents with coastal headlands or undersea banks may be responsible for dense aggregations of several species of fishes, including widow rockfish, *Sebastes entomelas*, in the northeastern Pacific and orange roughy, *Hoplostethus atlanticus*, off New Zealand (Robertson and Grimes 1983).

Similar mechanisms of aggregation probably exist for seamounts. Hamner and Hauri (1981) have described the aggregation mechanism for a small reef, which may be analogous to an isolated seamount. In open ocean areas, where eddies have been studied, the results are equivocal; Hall and Quill (1983) observed increased sound scattering inside as compared to outside an eddy in two out of three instances. Most studies of ocean eddies, however, deal with moving eddies which often differ faunistically from the surrounding water (Griffiths and Brandt 1983) and may thus differ from those in seamount areas. Eddy research is a relatively new field and the effects on the biota are poorly understood (Owen 1981; Angel and Fasham 1983). Pelagic sampling of seamount-generated mesoscale eddies, especially for prey consumed by dominant species, will be important for understanding the mechanisms of enrichment. High abundances of micronekton may exist over seamounts, but these species may be seamount-associated rather than pelagic, such as the sternoptychid fish *Maurolicus muelleri* and the mysid *Gnathophausia longispina* over Hancock Seamount (Boehlert and Seki (1984).

MECHANISMS OF RECRUITMENT OF DEMERSAL POPULATIONS

Understanding recruitment mechanisms and variability will be critical to understanding the sustainability of seamount resources. Given the high density of virgin stocks (Table 1) and their apparent reliance on prey produced elsewhere, it is probable that space is not limiting, at least for pelagic armorhead. For pelagic armorhead, it is probable that recruitment varies from year to year in response to physical variability. Wetherall and Yong (1986) suggested that recruitment is independent of stock size over a wide range of stock sizes, and that interannual variability in recruitment is probably responsible for fluctuations in population size. This is supported in part by calculations of recruitment from Borets (1975; Table 1). One of the first suggestions of a mechanism for recruitment in seamount populations invoked the concept of stationary Taylor columns over seamounts for maintenance of pelagic larvae (Shomura and Barkley 1979). This is an extension of the ideas on the conservation of insular plankton described by Boden (1952). Others have suggested that seamount populations are derived from upstream source populations; the distances proposed have been as great as 1,100 nmi (Lutjeharms and Heydorn 1981b). This could be the case for the populations of *M. muelleri* on Hancock Seamount; large populations are present in waters of Japan (Okiyama 1981) and advection in the Kuroshio could bring them to the area of the seamount in 100-200 days (K. Mizuno, Tohoku Regional Fish. Res. Lab., Shiogama, Japan). Similar advective mechanisms may link the seamount population of alfonsin, *Beryx splendens*, to that in Japan.

Potential recruitment mechanisms must be a function of the physical oceanography and life histories of the species concerned. The physical oceanography of the SE-NHR region, including dominant effects of the North Pacific Current and the Kuroshio Extension, is complex (Fig. 1). The existence of eddies in the region has been discussed. As the currents impinge upon the Emperor Seamounts, there is a change in the hydrographic pattern, including major differences in dynamic height perturbations and current flow east as compared to west of the chain (Roden 1977; Roden et al. 1982). The region of the SE-NHR seamounts, however, is also in the subtropical Pacific front. This front is best developed from late fall to early summer (Roden 1980) and eddies are shed along the front (Roden 1981). Mizuno and White (1983) have demonstrated that interannual variations exist in the latitudinal position of the Kuroshio, and thus the position of the front, resulting in variability in eddy production. Further south, at lat. 20°-24°N, is the Subtropical Countercurrent, which could conceivably transport pelagic eggs and larvae back to Japanese waters (Uda 1970).

Whereas the effects of seamounts on large scale flow have been described, the smaller scale effects have been largely inferred due to the scale of sampling (Roden 1986). Flow perturbations in the regions of the seamounts suggest eddy formation, and indeed satellite-tracked drifters have become trapped in eddies over seamounts (Cheney et al. 1980; Richardson 1980; Lutjeharms and Heydorn 1981b). Current flow patterns over the seamounts may thus vary with seamount morphology, ocean current strength, and season.

From a biological standpoint, research must be initiated to fill important gaps in our knowledge of the life history and behavior of the species of interest. Larval, pelagic, juvenile (Borets 1979) and benthic adult pelagic armorhead and alfonsin have been captured, but distribution of the intervening stages is unclear; in any case, the pelagic young stages of both species are relatively rare.

Humphreys et al. (1984) have described the current knowledge on life histories of pelagic armorhead and alfonsin. Young alfonsin apparently are recruited to the seamounts at an age of approximately 1 year after a pelagic larval stage (Chikuni 1971). It has been suggested that pelagic armorhead are recruited to seamounts after a largely pelagic existence, but the duration of this period is in question. Soviet scientists have suggested that recruitment to the seamounts occurs at an age of 6-9 years (Vasil'kov and Borets 1978), whereas the Japanese suggested that recruitment occurs at ages of 4-5 (Chikuni 1971). These ages were determined from different methods of scale reading. Our best estimates of age at recruitment for more recent samples suggest ages of 2-3 years, and the majority of recruits are 2-year olds (J. H. Uchiyama, Southwest Fish. Center Honolulu Lab.). All of these samples, however, have been taken with sampling gear for larger fish; virtually no sampling has been conducted on the seamounts which would collect small juveniles of either species. The recent discovery of large scale nursery areas for juvenile rockfish, *Sebastes* spp., in untrawlable areas in the coastal waters of Alaska required the use of a research submersible (Carlson and Straty 1981). In situ observation from a submersible, photographic transects, or other unconventional sampling techniques may thus be necessary to assess the presence and abundance of these important life history stages and to allow a fuller understanding of the recruitment process.

Knowing the duration of the pelagic period will allow better suggestions of recruitment mechanisms. The recruitment mechanism using Taylor columns as suggested by Shomura and Barkley (1979), for example, would probably require a relatively short-lived pelagic dispersal stage but could result in localized stocks or populations on individual seamounts. Eide (1979) noted trapped eddies over banks on the continental shelf off Norway, and Sundby (1984) suggested that these features allow retention of pelagic cod eggs and larvae sufficiently long for recruitment. A similar mechanism has been suggested for Georges Bank (Smith and Morse 1985). Alternatively, some species may have very extensive pelagic dispersal stages with different recruitment mechanisms, thus resulting in mixed stocks. Lutjeharms and Heydorn (1981b) suggested that rock lobster, *Jasus tristani*, is recruited to Vema Seamount after 9 months of pelagic drifting over some 1,100 nmi. Despite the long distance over which recruitment occurs, however, the mechanism is sufficiently robust to allow large-scale recruitment of depleted populations in relatively short periods of time (Lutjeharms and Heydorn 1981a).

The geographic distribution of a species may often provide an idea of the length of larval life and dispersal capabilities. Pelagic armorhead have now been divided to Northern and Southern Hemisphere species (*Pseudopentaceros wheeleri* and *P. richardsoni*, respectively; Hardy 1983). *Pseudopentaceros wheeleri* has been captured throughout the North Pacific (Fujii 1986) but is abundant only in localized regions such as the SE-NHR seamounts. The presumed long pelagic period of this species (2-3 years) allows such long-range dispersal but calls into question the mechanism of recruitment to the population centers. It may be that the physical factors responsible for enhancing productivity or aggregating prey over seamounts may also provide clues to their locations. If our interpretation of the long pelagic period is correct, it is probable that a single stock exists on the seamounts, as preliminary electrophoretic results suggest.

It is of interest to note that the orange roughy, *Hoplostethus atlanticus*, another deepwater fishery species, has a distribution pattern analogous to that of the pelagic armorhead (Robertson and Grimes 1983). Thus effects associated with other topographic features such as banks and islands (Uda and Ishino 1958) should also be investigated.

FUTURE RESEARCH DIRECTIONS

I will divide my suggestions of future research to those addressing strictly resource-associated questions and those of a more general nature dealing with mechanistic questions. The latter research areas, which I would define as relating to the general phenomena of high productivity or enrichment over seamounts, are generally beyond the logistic and financial contraints of the resource agencies and will need to be approached on a larger, multidisciplinary scale. The resource questions, although related, by necessity take a somewhat narrower approach, using available research vessels and fisheries data.

Research related to the resource issues must address the basic questions necessary for management of the fishery and will require a combination of research on stock structure, reproduction and behavioral biology, life history, and population assessment. Research on stock structure and species separation (particularly for *Pseudopentaceros*) should begin immediately to complete the preliminary work done and to allow interpretation and planning of other work. The research design should include work on pelagic armorhead and alfonsin. For pelagic armorhead, the questions include stock differences among seamounts (which preliminary electrophoretic information suggests do not differ), between fat and lean types, and between benthic and pelagic groups. It would also be of interest to compare Northern and Southern Hemisphere specimens to aid in our understanding of the taxonomic issues and species descriptions recently published by Hardy (1983). For the alfonsin, no work has been conducted to date on stock differentiation, but it would be interesting to determine if stock differences exist among seamounts and also the relationship of seamount and the western Pacific populations described by Yamamoto (1986). The apparent transport of Japanese sardine, *Sardinops melanosticta*, to the Emperor Seamounts (Yasui 1986), provides a mechanism for transport of early life stages of alfonsin from Japanese waters to the seamount region.

As described above, a wide variety of research on life history and biology of the dominant species will be of interest. The conceptual model of pelagic armorhead life history proposed by Humphreys and Tagami (1986), for example, has many unknowns which could be tested. Another key area of interest will be a study of the spawning and early life history of the two dominant species. Pelagic armorhead spawn during winter, alfonsin during summer. Do the larval distributions differ in response to the seasonal differences in physical oceanography? Can larvae be captured in sufficient numbers to meaningfully describe the effects of currents on distribution and dispersion? Plankton surveys should be conducted which consider the vertical distribution as it relates to water column structure and horizontal distribution as it relates to the seamounts and current flow patterns. What are the recruitment strategies of these two species? Is recruitment seasonal, as is spawning? Is the Taylor column concept realistic as a mechanism for the maintenance of pelagic populations? Many of these questions can only be addressed with the help of sophisticated analysis of physical oceanography to support our understanding of the biological oceanography.

Research must also be conducted to develop a better understanding of the habitat on the seamounts and the behavior of the dominant species. What is the diel activity pattern of each species? Our current ideas of the age at recruitment are based upon captures in experimental and commercial gear, which are notoriously poor for capturing juvenile stages. It is possible that younger specimens are recruited to the seamounts but are not available to our current sampling. Alfonsin may segregate to different habitats by age or size, as described by Seki and Tagami (1986). Submersible research could elucidate several aspects of the biology, habitat, and behavior of alfonsin and pelagic armorhead on the seamounts and allow a more comprehensive understanding of data collected using conventional shipboard methods. In several areas, for example, fish are apparently abundant in regions with high relief which prevent effective trawling operations (Yamamoto et al. 1978). Survey of these areas may allow more complete assessment of the populations and also provide information on the presence of juveniles and the nature of juvenile habitat (Uzmann et al. 1977; Carlson and Straty 1981).

Population age structure must also be determined. Based upon the ages determined in different studies, it is apparent that age validation work must be completed before a full study is undertaken. In armorhead, we must develop growth curves which will include the rare, larger specimens as well as curves based upon the dominant commercial sizes, which are apparently dominated by 2- and 3-year olds. Also, capture of the smallest specimens, whether in surface collections or from submersible benthic juvenile habitat will be necessary to aid our understanding of the growth dynamics; what percentage of somatic growth occurs before recruitment to seamounts? By considering the variability in age structure from year to year and the relationship with fish morphology, we may be able to estimate the variability in recruitment from year to year. If armorhead recruitment to seamounts occurs at later ages, as currently appears probable, then there are several points in the life history where variability in recruitment or year class strength could be influenced. Very strong recruitment, for example, apparently occurred in 1972 (Borets 1975; Takahashi and Sasaki 1977; Wetherall and Yong 1986). What is the role of recruitment variability in population abundance? Can we identify environmental features which may be responsible for recruitment variability? Physical and biological factors during the pelagic phase may play a role. Based on data from 11 years between 1969 and 1981 (in Humphreys et al. 1984), there is a negative correlation ($r = -0.77$) between catch per unit effort and mean length of armorhead. This suggests that density-dependent growth may occur in the pelagic environment.

Continued data collection will be necessary for population assessment. The fisheries-dependent model developed by Wetherall and Yong (1986) should be refined as more data become available and as the above research results allow better interpretation of existing data. Some level of continued fishing effort is desirable to allow model updating, stock monitoring, and development of biomass estimates. As ancillary goals, however, we should attempt some level of fisheries-independent resource assessment. At present, we have no ideas on changes in catchability that may have occurred through the history of the fishery. We should pay particular attention to methods such as hydroacoustic assessment, which could provide further information on the behavior of the species as well as fishery-independent assessment which could cover relatively large areas during daytime when the fish are unavailable to the trawl.

A major resource-related question concerns the trophic relationship of pelagic and demersal species. Preliminary work suggests that pelagic armorhead and alfonsin share similar prey resources. Is this resource base also common with the dominant pelagic species, including albacore, skipjack tuna, and squid? If so, have stocks of any of these potential competitors increased as pelagic armorhead stocks declined? The increased catch of alfonsin is suggested by Sasaki (1986) to reflect a change in targeted species by fishermen. We should also consider the speculation raised in the workshop discussion by Sasaki, namely, that pelagic armorhead use seamounts for spawning and that the "fat" condition developed in the pelagic environment deteriorates there due to lack of food. This speculation could be treated as a testable hypothesis, namely that insufficient food resources exist to maintain the virgin populations. An ecosystem model of a specific seamount would provide a means of addressing these issues.

The questions of seamount productivity should be addressed as a mechanistic phenomenon in a multidisciplinary fashion with key contributions from biological and physical oceanography. The general research question is "What are the factors important in maintaining large populations on seamounts?" This question should be addressed, as mentioned above, as one of productivity versus advection and convergence. Not all seamounts or banks would be classified as highly productive. Is the pattern of the SE-NHR seamounts a general phenomenon, with the energy simply channeled to other trophic levels or ecosystems, or are there specific features necessary for a highly productive seamount? If the latter is true, what are the features necessary to define a productive versus a nonproductive seamount? If we can define these features, it may be possible to describe areas in the sea where fisheries production may be unexpectedly high. The deep sea has traditionally been viewed as relatively low in production and biomass, but the development of the orange roughy fishery in New Zealand at depths from 800 to 1,200 m is currently providing an annual harvest in excess of 30,000 MT (Robertson and Grimes 1983). Thus knowledge of the factors important in productivity of deeper waters may aid in searching deepwater areas where resource exploration has not been conducted.

Research of this nature will require a variety of research disciplines. First, physical oceanographic studies based on closely spaced sampling grids as proposed by Roden (1986) will need to determine the conditions for development of eddies, Taylor columns, fronts, and other mesoscale features of flow complexity. Also, since we are interested in productivity effects in the euphotic zone, we must consider how these effects transfer into the mixed layer. Further research with moored current meter arrays, satellite- or radio-tracked drogues, and remote sensing will allow definition of the seasonal nature of variability in these mesoscale features. Are these features consistent within season, from year to year? What role is played by interannual variability of the kind described by Mizuno and White (1983)? Given the bottom topography and information on ocean currents, can one predict locations of eddies or gyres?

A variety of research on the biological oceanography of the water columns over seamounts is also of interest. What is the variability of primary productivity in the region of seamounts? Can a signal be detected in the levels of primary productivity associated with seamounts and if so, what is the residence time and consistency of such productivity? If enhanced productivity is present, however, further work will be necessary to demonstrate whether it is advected away or remains in the region for transfer to higher trophic levels of both fishes and benthos. Also, if there is no signal in primary productivity, can we assume that convergence and aggregation are responsible for seamounts with high biomass? As this question is considered, it should be related to areas other than seamounts, including banks (Uda and Ishino 1958), coastal headlands (Alldredge and Hamner 1980), and islands (Boden 1952; Hamner and Hauri 1981), where similar phenomena may occur.

Secondary productivity studies and descriptions of the spatial distribution and abundance of plankton and nekton will also be necessary. What is the mechanism of vertical flux of materials from surface waters to the seamounts? The dominant fish species of the SE-NHR seamounts apparently forage in the water column (Sakiura 1972; Borets 1979); is the mechanism of vertical transport a biologically mediated one? Do the benthos of seamounts show enrichment relative to shelf-slope biomass values, and if so, what is the energy source? We should undertake trophic studies which will allow better description of the ecosystem interactions in seamount regions. In this manner, preliminary models of the energy flow and higher trophic level production could be estimated. Does the combination of virgin stocks of demersal seamount populations and the pelagic populations require higher energy levels than average regional primary productivity would indicate? This may be a productive preliminary approach to assessing research questions on seamount oceanography.

In conclusion, seamounts represent an ocean feature whose potential for biological resources has been largely overlooked. Although seamounts may never represent a major contribution to world fishery resources, rational exploitation of the seamount resources requires a great deal of information before we can expect management to sustain populations. The armorhead is characterized by a broad feeding range, a wide variety of prey organisms, rapid growth, and early maturity. These features suggest that proper management of this resource could result in a significant, sustainable yield. The scientific questions associated with seamount oceanography and productivity are important to understanding the dynamics of seamount ecosystems.

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Energetics during embryonic development in kurosoi, *Sebastes schlegeli* Hilgendorf

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Abstract: Studies on the live-bearing scorpaenid genus *Sebastes* have recently shown that embryos of one species receive nutrition in addition to that supplied in the yolk. In this large genus, however, reproductive characteristics may differ among species. Energetics of embryonic development in kurosoi, *Sebastes schlegeli* Hilgendorf, were analyzed to determine the patterns of embryonic nutrition. The egg of this species is larger and contains over three times the energy content of that in *S. melanops*, another species which has been studied. Catabolism during the 51 days of embryonic development required 88% of the original energy in the egg, but the embryo at birth contained 93% of the initial egg energy. Thus the total energy required for development from fertilization to birth requires ≈ 1.8 times the initial, endogenous energy supply. Histological studies demonstrate that uptake occurs through ingestion and absorption of ovarian fluid in the hindgut. Protein and nitrogen budgets during development suggest that the primary substance taken up is nitrogenous.

No distinct structures are apparent in the ovarian system to supply nutrients to the developing embryos. Analysis of fecundity-at-length, however, shows that post-fertilization fecundity estimates are significantly lower than pre-fertilization values; the reduction apparently occurs through resorption of ova or early embryos. Along with catabolism, this results in an overall decrease in the energy content of the ovaries during development, but the total amounts of protein and nitrogen remain nearly static. We thus suggest that resorption of unfertilized ova or early embryos which die may enrich the ovarian fluid and supply energy to the surviving embryos. This is a primitive form of embryonic nutrition in viviparous species and may be common in the genus *Sebastes*.

Key words: Reproduction; Embryo; Energetics; Respiration; Viviparity; *Sebastes*

INTRODUCTION

Reproduction in the live-bearing genus *Sebastes* has historically been considered to be lecithotrophic viviparity, with the only parental care provided as a form of embryonic protection (Balon, 1975) rather than a nutritional association between female and embryo (Needham, 1942; Scrimshaw, 1945). The reasons for this description have not been based on energetic studies but rather on inference; initial egg size is small, larvae are small at birth, and fecundity is very high (Phillips, 1964; Moser *et al.*, 1977; Boehlert *et al.*, 1982). Recently, however, Boehlert & Yoklavich (1984) have shown that embryos

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of the black rockfish, *S. melanops*, derive some form of nutrition from the maternal system during later stages of the approximately 37-day gestation period. They suggested that the source of nutrition was a nitrogenous substance, because nitrogen content remained static during development, in contrast to oviparous species (Hayes, 1949; Rogers & Westin, 1981). The suggested mechanism of nutrition was through ingestion of ovarian fluid and subsequent uptake in the hindgut (Boehlert & Yoklavich, 1984). This mechanism is suggested to be one of the earliest in the evolution of viviparity (Wourms, 1981).

The genus *Sebastes* has over 100 species (Barsukov, 1981); there is thus a question of how representative the results from a single species are to the reproductive pattern in the genus. In the live-bearing poeciliids, for example, Thibault & Schultz (1978) observed remarkable variation within a single genus. Considering the ratio of dry weight of developed embryo at birth to that of the egg at fertilization in the genus *Poeciliopsis*, they noted values from 0.61 to 19, demonstrating a range from lecithotrophic to matrotrophic viviparity. More recent work has demonstrated both spatial and temporal population-level differences in the type of viviparity in *Poecilia latipinna* (Trexler, 1985).

Considerable differences exist in initial egg size, larval size at birth, and weight-specific fecundity in the genus *Sebastes*. *Sebastes melanops* has an egg diameter of 0.8 mm at fertilization (Boehlert & Yoklavich, 1984), typical of the small (≈ 1 mm) eggs of eastern Pacific species (Moser *et al.*, 1977). Eastern Pacific species were previously considered to be a different genus (*Sebastodes*) to Atlantic and western Pacific species but were combined by Matsubara (1943), whose interpretation was supported by Chen (1971). Western Pacific species generally have larger eggs (to 1.5 mm in *S. pachycephalus*, Fujita, 1957). Advanced viviparous species typically have very small eggs at fertilization and rely upon maternal nutrition for embryonic development (Turner, 1947; Thibault & Schultz, 1978). Thus within a genus it might be advantageous to compare species with different egg sizes; in this study we describe embryonic energetics and development of kurosoi, *Sebastes schlegeli* Hilgendorf, from Japan.

Sebastes schlegeli is a coastal species which inhabits rocky reefs and is found from depths of 30 to 100 m. It is relatively docile in aquaria, has an egg size of ≈ 1.2 mm, and larvae may be reared; it is thus considered a species with aquaculture potential in Japan (Kusakari *et al.*, 1977; Kusakari, 1978). Shimizu & Yamada (1980) considered ultrastructural aspects of yolk utilization in the vitelline syncytium and suggested that the pattern was similar to that in oviparous fishes. They did note, however, an opaque substance in the hindgut in late stage embryos, a situation analogous to that in *S. melanops* (Boehlert & Yoklavich, 1984). This suggests that a similar mechanism for nutritional uptake may exist in this species.

MATERIALS AND METHODS

EXPERIMENTAL ANIMALS

Experiments were conducted during May 1984, the typical spawning season for this species. Fish were held in 1.1 m by 1.8 m tanks at the Hokkaido Institute of Mariculture, Shikabe, Hokkaido, Japan, where they were subject to ambient temperature. Most fish were laboratory broodstock which had been held for long intervals, but additional females were also captured near Otobe in the Sea of Japan shortly prior to the experiments. Since temperature control was not available for the large holding tanks, females were held throughout the experiments at ambient temperature, which fluctuated between 4.6 and 7.3 °C.

Before experiments, all females were anesthetized in ethane methanesulfonate (MS-222, Argent), weighed, tagged with an identifying number, and embryos removed from the ovary by gentle catheterization for determination of stage of development. Developmental stages were classified according to a modification of Oppenheimer (1937) and Yamada (1963) (Kusakari, unpubl. data).

LABORATORY PROCEDURES

Laboratory procedures generally followed Boehlert & Yoklavich (1984). Gestation time and duration of different stages of development were determined from several measurements on 55 females held in the laboratory during 1983. Although temperature in the tanks varied between 8.0 and 13.6 °C during this time, the mean temperature was 10.6 °C (SD 1.48 °C). Fish were catheterized at times t_1 and t_2, and the corresponding developmental stages determined as S_1 and S_2, respectively. The data points

$$\frac{S_1 + S_2}{2}, \frac{t_2 - t_1}{S_2 - S_1},$$

or mean stage (S) and stage duration (D) in days, were plotted and a curve fitted to the data. Only those observations separated by 7 days or more were used in these calculations.

Oxygen consumption was determined for embryos at several stages of development. Embryos were removed from the female and placed in isosmotic saline (340 mosM/kg, Wasserman *et al.*, 1953) in a 15-ml respirometer flask; numbers of embryos per flask ranged from 45 to 267. After equilibration of temperature for ≈ 1 h, oxygen consumption (Q) was measured on a Gilson[1] differential respirometer at 10 °C using standard techniques (Umbreit *et al.*, 1972). Except when readings were taken, lights were kept off during experiments. Experiments were run between 1000 and 2000 h. Values of oxygen consumption (μl O_2) were recorded at approximately hourly intervals and experiments lasted from 3 to 8.2 h. Two or three control flasks were run concurrently with each experiment and control values were subtracted from readings in experimental flasks. At the end of each experiment, the embryos were counted and used for dry weight and carbon and nitrogen determinations, and some embryos were preserved for determination of developmental stage. Ash-free dry weight (AFDW) was determined from groups of 35–100 embryos dried at 58 °C to constant weight (on aluminium foil), cooled to room temperature in a desiccator, and weighed. They were ashed for 4 h at 500 °C and ash weight determined. Carbon and nitrogen content were determined in a Hewlett-Packard Model 185 CHN analyzer. All values were means of duplicate samples. Caloric content was determined from percent carbon using the nitrogen-corrected equation of Salonen *et al.* (1976) following Boehlert & Yoklavich (1984). Protein was determined using Lowry's method (Lowry *et al.*, 1951), and protein nitrogen was determined by dividing this value by 6.25. Embryos were fixed in glutaraldehyde in saline and prepared for scanning electron microscopy using standard techniques (Dobbs, 1974; Boehlert, 1984) and were observed under a JEOL JSM-2F SEM. Transmission electron microscopy followed Shimizu & Yamada (1980) with 1.5 h fixative in a paraformaldehyde–glutaraldehyde mixture (Karnovsky, 1965) and post-fixation in 1% osmium tetraoxide in phosphate buffer for 1 h. Ultrathin sections were doubly stained with uranylacetate and lead citrate and observations were made with a Hitachi HU-12 electron microscope.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Stage duration calculations were based upon initial (S_1) stages from 4 to 31, and final (S_2) stages from 21 to birth. Earliest stages, which are passed through rapidly, were least represented in our estimates of stage duration (D). These data were linearized and fitted to an exponential model with the resulting relationship;

$$D = 0.02535\ S^{1.4333} \qquad n = 55 \qquad r^2 = 0.67 \text{ (Fig. 1).}$$

This curve (solid line) suggests that early stages are passed through very rapidly whereas later stages may take as long as 3.6 days. The area under this curve was integrated to give the dashed line, time since fertilization (T, days) as a function of developmental stage (S). The equation is

$$T = 0.0104S^{2.4333}.$$

This relationship predicts that fertilization to birth (Stage 33) takes 51.5 days. Observations of three females from 1983 suggest a mean gestation time of 46 days but range from 42 to 50 days. This period may therefore be somewhat variable under natural conditions.

Oxygen consumption was determined from embryos at 16 stages of development and showed an exponential increase with time since fertilization (Fig. 2). Earliest embryos (Stage 8, 1.6 days post-fertilization) showed very low oxygen consumption rates, with a mean value of 0.0181 μl $O_2 \cdot \text{embryo}^{-1} \cdot h^{-1}$, whereas the latest stages tested (Stage 31.5, 46 days post-fertilization) had mean oxygen consumption of 0.6688 μl $O_2 \cdot \text{embryo}^{-1} \cdot h^{-1}$. Groups of the earliest embryos tested, when counted at the end of our experiments, were often characterized by a percentage of eggs which enlarged (and perhaps died) in the saline. To assess potential effects on respiration, eggs were allowed to remain in saline, and groups of enlarged ones placed in respirometers; oxygen consumption did not differ, however, between the "enlarged" and normal eggs. For embryos in the latest stages of development, limited swimming activity occurred in the flasks; thus our values for late stage embryos may be slightly inflated.

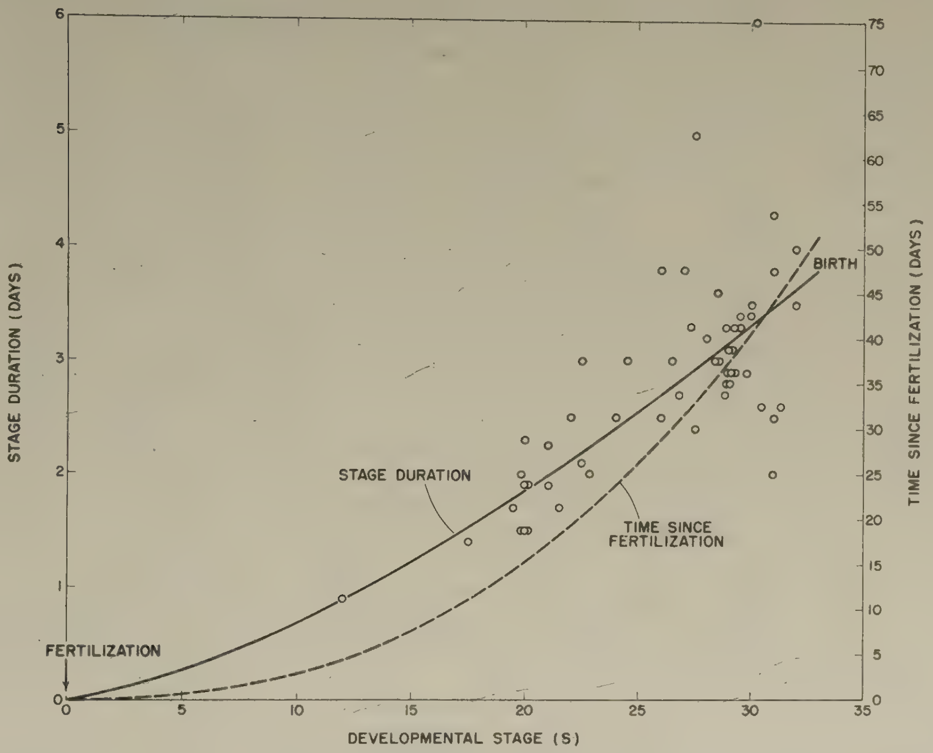

Fig. 1. Gestation time in *Sebastes schlegeli*, showing how long it takes to get to any given stage from fertilization: the calculations are based on the method of successive catheterization developed by Boehlert & Yoklavich (1984); stages follow Kusakari's modification of Oppenheimer (1937); here, Stage 33 represents birth; the estimated time from fertilization to birth is 51.5 days.

The curve fitted to the linearized oxygen consumption data is represented by

$$Q = 0.02188e^{0.07012T} \qquad n = 16 \qquad r^2 = 0.96 \text{ (Fig. 2)}.$$

This curve was integrated to estimate the total oxygen consumed (Q_T) as a function of time since fertilization, resulting in the equation

$$Q_T = 7.4889e^{0.002922H},$$

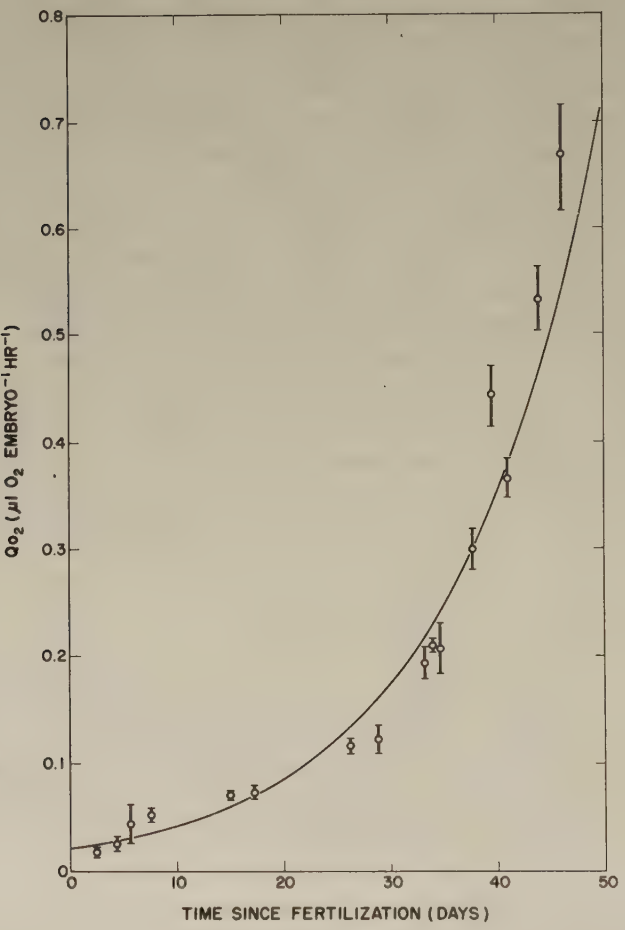

Fig. 2. Oxygen consumption in embryonic *Sebastes schlegeli*: the numbers of embryos varied between 45 and 267; there were generally more used in experiments with early stage embryos; experiments were run in a Gilson differential respirometer at 10 °C; each point (± 2 SE) represents the mean of three or four replicates from embryos from the same female.

where H = time since fertilization in hours. This relationship suggests that an embryo would consume a cumulative total of 277 μl O_2 during development from fertilization to birth. This value, converted to calories using the oxycalorific equivalent of 0.005 cal $\cdot$ μl O_2^{-1} (Lasker, 1962), suggests that catabolism during gestation requires 1.386 cal.

Embryo weight and AFDW were estimated for 13 stages throughout gestation (Fig. 3A). Ash content generally increased with time since fertilization; the mean value was 8.5% dry weight. Our data suggest increasing AFDW (μg) with time since fertilization, with the fitted curve

$$\text{AFDW } (\mu\text{g}) = 255.8 + 1.086T \qquad n = 13 \qquad r^2 = 0.40.$$

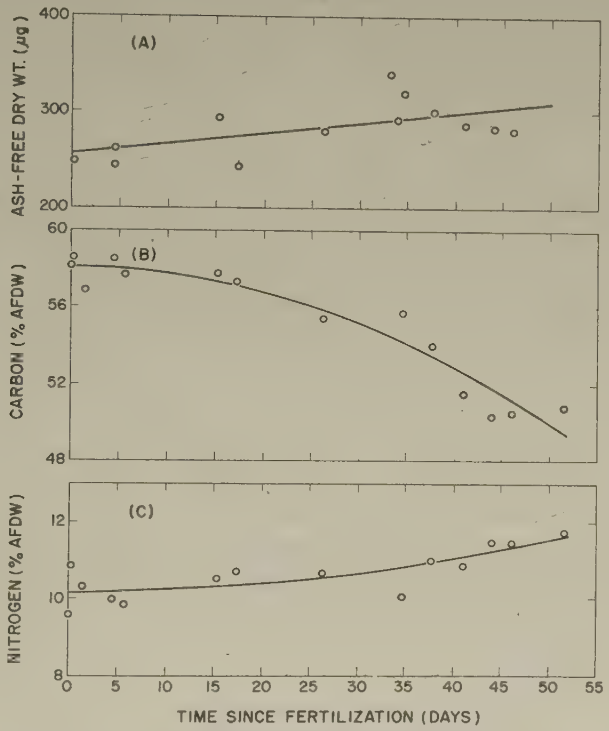

Fig. 3. Changes in ash-free dry weight (AFDW) (A), carbon (B), and nitrogen (C) as a function of time since fertilization (days): carbon and nitrogen are both expressed as percentages of AFDW; the increase in AFDW and nitrogen and the decrease in carbon are all significant.

A concern with this relationship is the source of weight increase. It is possible, for example, that older, larger females have larger embryos at all stages, as observed in some other species (Bagenal, 1971). If this were the case, and if larger females were fertilized earliest in the season, then the observed relation could be an artifact. To test for this, we regressed embryo weight on female length. The relationship was not significant ($n = 13$, $P > 0.25$). We thus concluded that the increase in weight is a function of time since fertilization rather than female size.

Carbon and nitrogen were determined as a percentage of AFDW. Carbon decreases as a function of time since fertilization (T) by the fitted curve

$$\%\,\text{C} = 58.09 - 0.003272(T)^2 \qquad n = 14 \qquad r^2 = 0.92 \text{ (Fig. 3B).}$$

The decrease is highly significant. The carbon content at fertilization was converted to a caloric value of 1.59 cal using the formula from Salonen *et al.* (1976). The opposite trend occurs for nitrogen which shows a significant increase with time since fertilization, described by the curve

$$\%\,\mathrm{N} = 10.16 + 0.000533(T)^2 \qquad n = 14 \qquad r^2 = 0.64 \text{ (Fig. 3C).}$$

The increasing AFDW and increasing % N combine to result in a marked increase in nitrogen over the course of development.

Protein was determined for embryos at 12 stages and increased during development. The relationship is described by

$$\mu\mathrm{g\ protein} = 148.52 + 0.862T \qquad n = 12 \qquad r^2 = 0.75,$$

which predicts an increase of 44 μg protein over the 51.5-day gestation period. Thus protein accounts for ≈80% of the weight gain of AFDW over development (Fig. 3A), suggesting that protein is the major source of maternal nutrition in this species. Protein nitrogen, calculated by dividing protein by 6.25, increases linearly but not as fast as total nitrogen (Fig. 4). Based upon the curves for AFDW and nitrogen (Fig. 3A,C), total nitrogen increases from 26.0 μg at fertilization to 36.1 μg at birth, whereas protein nitrogen increases from 24.5 μg to only 30.5 μg (Fig. 4). Thus non-protein nitrogen increases from 5.7 to 15.3% during development, suggesting that nutrition from the maternal system may also include amino acids and peptides in addition to protein. The same phenomenon was observed for *S. melanops* (Boehlert & Yoklavich, 1984).

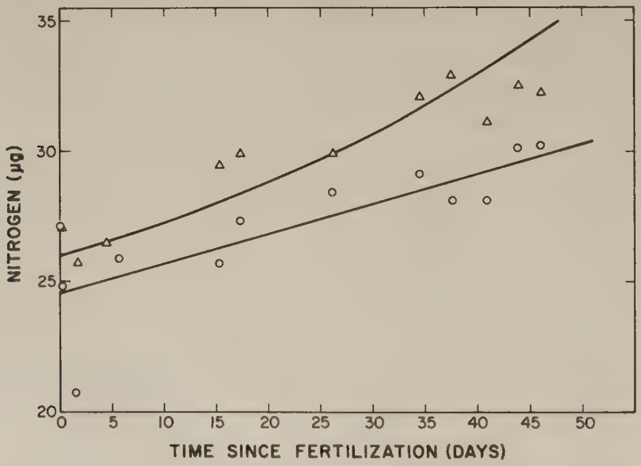

Fig. 4. Changes in nitrogen content of embryonic *Sebastes schlegeli* as a function of time since fertilization: the lower curve and points represent protein nitrogen (protein/6.25); the upper curve represents total nitrogen determined by CHN analysis.

A comparison of catabolic and calorimetric estimates of energetics of embryonic development in *S. schlegeli* shows different patterns (Fig. 5) similar to that observed in *S. melanops* Girard. The catabolic energy usage is calculated by considering the cumulative oxygen consumption (Fig. 2) and converting it to calories; the resulting values were subtracted from the total energy available in the egg at fertilization (1.59 cal). The catabolic energy utilization suggests that ≈12% of the original yolk energy remained at the end of development. The data points represent actual energetic data. Fitting a curve to these data suggests that ≈93% of the original energy remained at birth. The difference between the catabolic calculation (solid curve) and the actual calculation (dashed line) represents the maternal contribution to embryonic development. Our estimate of total energy necessary for each embryo is thus 2.87 cal (1.39 catabolic calories, 1.48 in larva at birth); this represents 1.8 times the initial energy content of the yolk at fertilization.

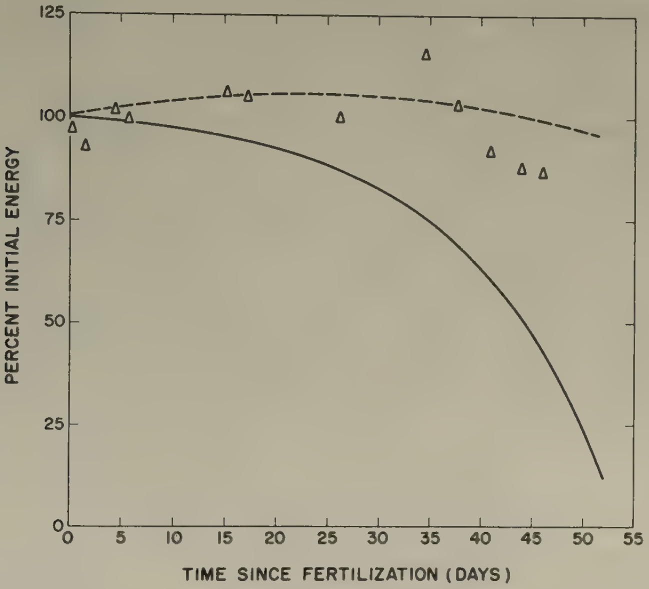

Fig. 5. Summary of the energetics of development in embryonic *Sebastes schlegeli*: the *y*-axis is the percent initial energy, where 100% represents 1.59 cal; the solid line represents expected energy remaining with time based on subtraction of cumulative catabolism; the dashed line and data points represent data from actual caloric content of embryos at different stages.

The mechanism of nutrient uptake in embryos of *S. schlegeli* was investigated by analyzing morphology. The epidermis of this species, when examined with scanning electron microscopy, shows microridges developing in early stages (Figs. 6A–C). They are particularly conspicuous in the dorsal head, yolk sac, and tail regions, scattered over the cell surface as irregularly arranged, discontinuous fragments. With advancing developmental stage, microridge development increases over the entire body

(Figs. 6D–E), but some cells have little or no microridge development (Fig. 6F). At Stage 28, smooth continuous microridges become apparent along the cell border, but nowhere is there evidence of microvilli, which typically characterize absorbtive surfaces (Veith, 1979). A very conspicuous cell type, the sacciform cell (Bullock, 1980), is highly abundant in the area underlying the epithelial cells. On the surface, they are evident as

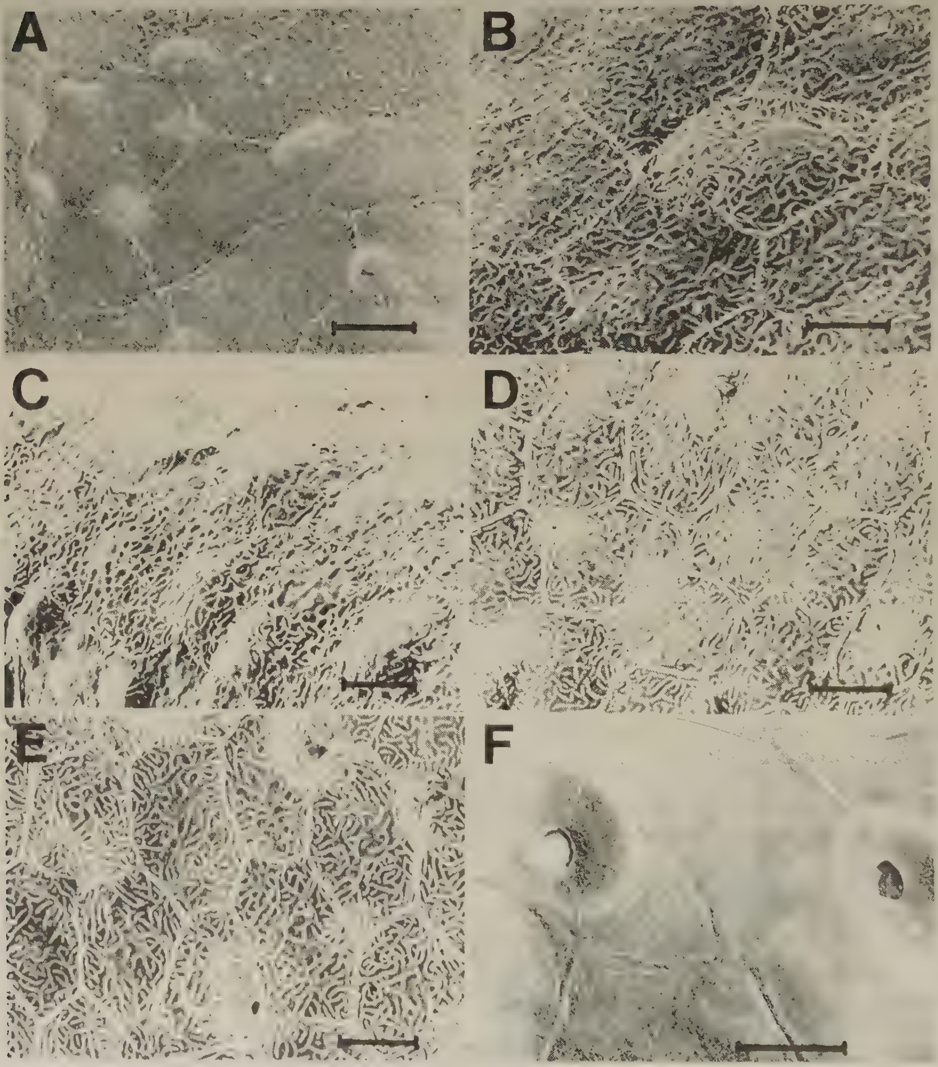

Fig. 6. Scánning electron microscopy of epidermis of embryonic *Sebastes schlegeli*: A, development Stage 24, dorsal surface of head; B, Stage 24, yolk sac surface; C, Stage 24; dorsal side of the tail finfold; D, Stage 28, dorsal surface of head; E, Stage 28, yolk sac surface; F, Stage 27, surface of the posterior part of the yolk sac corresponding to the site of an oil droplet; note the pores associated with the underlying sacciform cells; scale bars = 1 μm.

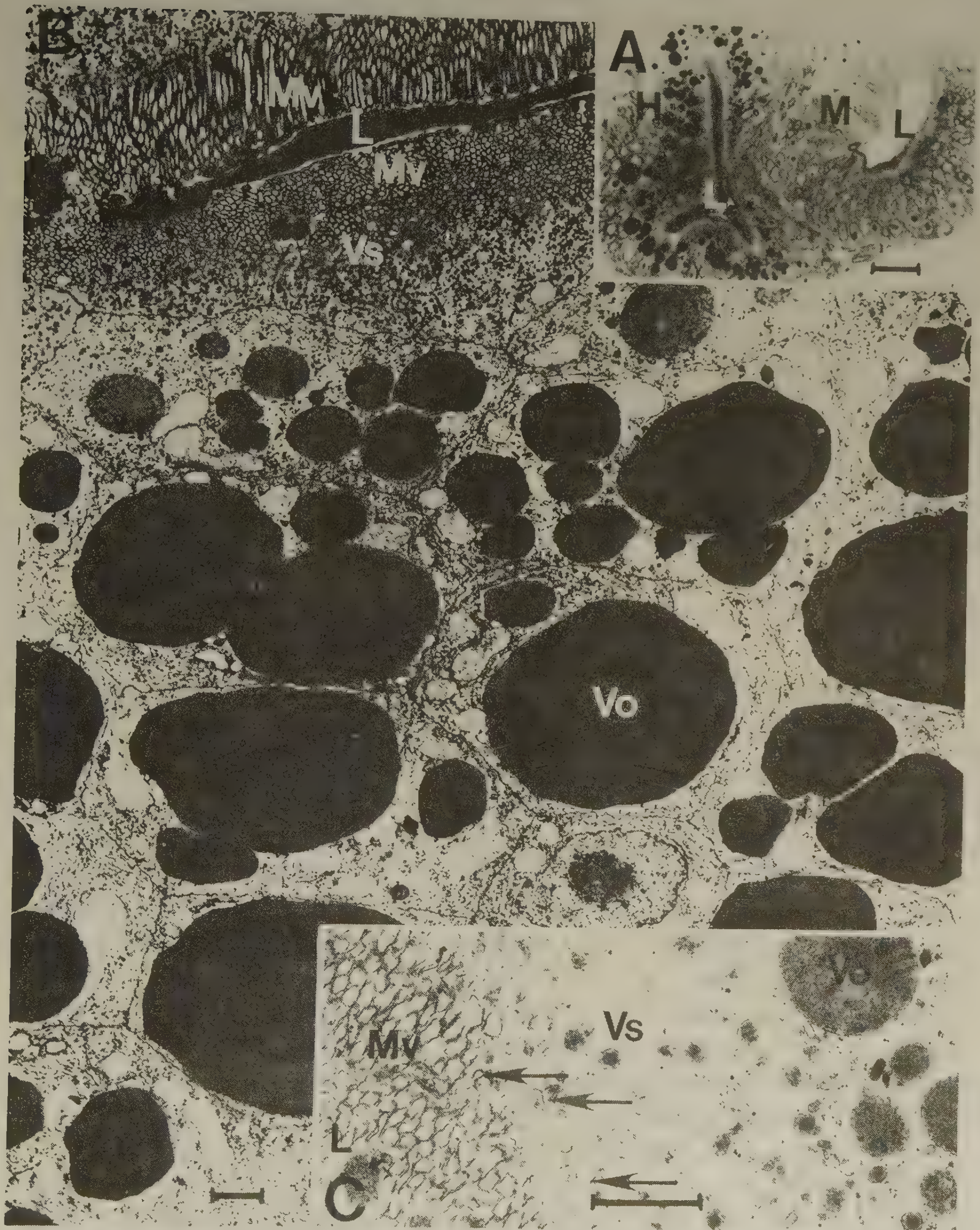

Fig. 7. Structures of the hindgut in embryonic *Sebastes schlegeli* at development Stage 28 (34.5 days post-fertilization); A, light micrograph of a 1 μm-thick Epon section of the hindgut (left) and midgut (right); methylene blue-azur II stain; scale bar = 20 μm; B, transmission electron micrograph of the apical part of the hindgut cells; scale bar = 1 μm; C, enlargement of the apical region of a hindgut cell; scale bar = 1 μm; H, hindgut; L, lumen; M, midgut; Mv, microvilli; Vo, vacuole; Vs, vesicle; arrows indicate pinocytotic invaginations between microvilli.

either swellings with central pits or depressions (Figs. 6A,C,D) or as pores (Fig. 6F). Their function in *S. schlegeli* embryos is unknown.

While we see no evidence of epidermal nutrient uptake, the gut is especially well developed in the hindgut region after opening of the mouth. We observed an opaque substance in the hindgut of developing embryos after mouth opening, as noted previously (Shimizu & Yamada, 1980). Under the microscope we observed movement of this substance within the gut and peristaltic movement in the hindgut region. Gut structure of Stage 28 embryos shows a high degree of development and apparent digestive activity (Fig. 7). The hindgut is characterized by many large vesicles not apparent in midgut tissue (Fig. 7A). Transmission electron microscope observations of hindgut cells show that the vesicles are variably sized and contain an electron dense, homogeneous substance, mostly distributed in the apical cytoplasm (Fig. 7B); it is likely that vacuolar contents in this part of the gut are proteinaceous (Watanabe, 1982). A number of tiny, round, or tubular vesicles are apparent under the microvillous cell surface facing the lumen, apparently forming from pinocytosis (Fig. 7C). These small vesicles merge to form larger ones as distance from the lumen increases (Fig. 7B,C).

DISCUSSION

The results of this study demonstrate that *S. schlegeli* embryos receive nutrition beyond that available in the yolk, consistent with the interpretation of Boehlert & Yoklavich (1984), who observed a similar pattern of embryonic energetics in *S. melanops*. The egg of this latter species has only 27% of the energy content of the larger egg of *S. schlegeli* at fertilization, and the gestation time at 10 °C is 37 compared with 51.5 days. Despite greater initial energy content, uptake of additional nutrition and energy in *S. schlegeli* is greater than in *S. melanops*, particularly for protein (Table I). Boehlert & Yoklavich (1984) suggested that the major source of uptake was protein or some other nitrogenous compound because total nitrogen remained static while protein decreased. Nitrogen utilization in early development may be generally true in fishes; Eldridge *et al.* (1982) pointed out that lipid is reserved until feeding begins in striped bass larvae. This might explain the increasing carbon/nitrogen ratio noted during development in this species (Rogers & Westin, 1981).

Our histological studies suggested that the hindgut was the location of nutrient uptake; the presence of an opaque substance in the lumen and the characteristic features of the hindgut cells (Fig. 7) indicated that the substance ingested into pinocytotic vesicles may undergo intracellular digestion. The hindgut region is where protein absorption occurs in fish larvae (Iwai, 1969; Tanaka, 1973; Watanabe, 1982; Govoni *et al.*, 1986). In *S. schlegeli*, nitrogen and protein both increase with development (Fig. 4; Table I), as supported by morphology of the hindgut (Fig. 7). We observed no evidence that epidermal cells are involved in nutrient uptake (Fig. 6), and the pattern and development of microridges were similar to those in medaka, an oviparous fish

(Yamada, 1966). The presence of a large number of sacciform cells, however, with openings to the epidermal surface deserves more study due to their unknown function. Thus, a similar, but perhaps more advanced mechanism of embryonic nutrition is present in *S. schlegeli* compared with *S. melanops*.

TABLE I

Changes in selected developmental features at the beginning and end of gestation in *Sebastes schlegeli* (present study), *S. melanops* (Boehlert & Yoklavich, 1984), and *S. caurinus* (Dygert, 1986): gestation times are 51.5, 37, and 41.5 days, respectively; PN/TN, protein nitrogen to total nitrogen ratio; C/N, carbon–nitrogen ratio; * near, but slightly after fertilization.

	Sebastes schlegeli		*Sebastes melanops*		*Sebastes caurinus*	
	Initial	Final	Initial	Final	Initial	Final
AFDW (μg)	255.8	311.7	67.5	60.4	160	127
Caloric content	1.59	1.48	0.429	0.345	1.05	0.69
Nitrogen (μg)	26.0	36.1	7.0	7.0	–	–
C/N ratio	5.72	4.27	5.74	4.80	–	–
Catabolic energy use (%)	0	88	0	64	0	38.9
Protein (μg)	148.5	192.9	45.3*	35.3	–	–
PN/TN	0.94	0.85	0.99*	0.73	–	–

A comparison of embryonic oxygen consumption by these two species suggests that it is greater in *S. schlegeli*, as would be expected on size considerations alone, but the relative consumption throughout gestation is also greater (Table I). The data for *S. schlegeli* are more complete than for *S. melanops* and reveal a marked exponential increase in later stages of development (Fig. 2). This agrees with data for *S. caurinus* embryos (Dygert, 1986). Several sources of error may occur in these estimates of oxygen consumption. In the present study, experiments were run at 10 °C but gravid females were held at lower, ambient temperatures. In juvenile *S. diploproa*, Boehlert (1978) distinguished between acute and acclimated changes in oxygen consumption rate between different temperatures and showed that different Q_{10} values characterize these different temperature changes. Applying the increased oxygen consumption values associated with acute temperature change suggests that values in the present study may be some 12% higher on average than if the females were held at 10 °C and thus acclimated to that temperature.

A second source of error in the measurement of oxygen consumption may be activity in later stages of embryos when removed from the maternal system. Differences in larval respiration rates between "active" and "inactive" Pacific sardine larvae may be from 1.3 to 3.5 times (Lasker & Theilacker, 1962). The third and perhaps most serious source of error in measurements of oxygen consumption for all three species (*S. schlegeli*, *S. melanops*, and *S. caurinus*) may be due to oxygen tension. Oxygen tension in the

Gilson respirometer is initially at saturated, atmospheric levels (Umbreit *et al.*, 1972). Oxygen tension inside the ovary is unknown, but *Sebastes* has a unique system of supplying arterial blood to both ovaries (Moser, 1967). Still, the ovaries in *Sebastes* are very large and later stage embryos must require a great deal of oxygen; diffusion from the vascularized ovarian wall must be important. Also, in the embiotocids *Rhacochilus vacca* and *Embiotoca lateralis*, Webb & Brett (1972) suggested that convection of embryonic fluid must occur. Still, for *S. schlegeli*, a 35-cm female with advanced embryos has estimated fecundity near 120 000 embryos (Kusakari, unpubl. data). Given the oxygen consumption rate of later larvae (Fig. 2), this could require oxygen delivery of some 40 ml/h to each ovary. Thus oxygen tension in the ovary may be reduced, a situation which may lower respiration rate in embryos (Carlson & Seifert, 1974). It is therefore possible that the rate of development of embryos may be under the control of oxygen availability and that the long gestation times and stage durations (Fig. 1) may be a result.

While all the above factors would operate to increase in vitro estimates of oxygen consumption and therefore our estimates of catabolic energy utilization, this does not change our conclusions. That is, the increasing AFDW (Fig. 3), protein content (Fig. 4, Table I), and hindgut development (Fig. 7) confirm that *S. schlegeli* is a matrotrophic vivipare. Nonetheless, it would be interesting to measure oxygen tension in the ovary and oxygen consumption of embryos at these values, if they are lower than saturation, and also to determine the developmental rate at saturation oxygen levels in vitro. Triplett (1960), for example, observed more rapid development, typically at smaller sizes in embiotocid embryos reared in vitro. These embryos come from an ovary with advanced structures for nutrient and respiratory gas exchange (Webb & Brett, 1972) and embryos have specialized spatulate median fins for gas exchange (Dobbs, 1975).

The source of the nutritional substance is an interesting question. *Sebastes* has no known specialized ovarian system for nutrient supply as seen in other viviparous fishes (Amoroso, 1960; Wourms, 1981), although the ovarian granulosa cells hypertrophy in the ovary of *S. paucispinis* (Moser, 1967). Boehlert & Yoklavich (1984) suggested that embryos resorbed after death in the ovary may be a source of such nutrition, since realized fecundity at birth is considerably lower than the fecundity estimates before fertilization (*S. marinus*, Raitt & Hall, 1967; *S. thompsoni*, Yoneyama, 1979; *S. entomelas*, Boehlert *et al.*, 1982). We noted atretic, post-fertilization embryos in *S. schlegeli*, particularly at early stages of development, and estimates of fecundity in *S. schlegeli* similarly differ for pre- and post-fertilization ovaries (Kusakari, unpubl. data), with typically lower fecundity at a given length for females with fertilized embryos. If these resorbing embryos represent the source of nutrition, this mechanism would be similar to the case of oophagy in elasmobranchs (Amoroso, 1960; Wourms, 1977). It would be interesting to note whether the decrease in fecundity provides sufficient energy to fuel the additional energy input to the remaining embryos. In a 35-cm (SL) fish, for example, the predicted difference in pre- and post-fertilization fecundity is $\approx 25\%$. Total ovarian embryonic energy content, embryo dry weight, and carbon all show significant declines in this situation (Table II). Nitrogen and protein, however, are nearly conserved since they increase in individual embryos during gestation (Figs. 3 and 4). It is thus possible that the resorption of embryos from the reduction in fecundity after fertilization provides nutrition for surviving embryos. Natural embryo death may be the cause of this reduction in fecundity. Vladimirov (1975) suggested the existence of genetic critical periods in embryonic development where heightened mortality occurs. Longwell & Hughes (1981) provide cytogenetic data supporting this argument in eggs of *Scomber scombrus*, finding chromosomal anomalies presumed to cause mortality. If high embryonic death is generally the case in *Sebastes*, viviparity is especially significant; rather than losing the energy in dead embryos as in oviparous species, it may be recovered by surviving broodmates, in turn increasing their chances of survival. The additional nutrition provided during gestation would thus come from within the ovary itself rather than being provided by new energy from the maternal system.

TABLE II

Estimated energy content of the ova and fully developed embryos of a 35-cm *Sebastes schlegeli* based on the fecundity change after fertilization: the fecundity relationships from 1979 data are as follows: pre-fertilized fecundity (range 25.8–38.8 cm SL, mean 33.6 cm SL): $\ln(F) = 5.824 + 0.1760(SL)$; ($n = 40$; $r^2 = 0.75$); post-fertilized fecundity (range 28.6–41.6 cm SL, mean 34.5 cm SL): $\ln(F) = 7.935 + 0.1072(SL)$; ($n = 24$; $r^2 = 0.67$), (AFDW = ash-free dry weight).

	At fertilization	At birth
Number of embryos	160 171	119 014
Energy (kcal)	254.17	176.28
Embryo AFDW (g)	40.89	37.12
Carbon (g)	23.75	18.34
Nitrogen (g)	4.15	4.30
Protein (g)	23.74	22.98

The evolution of viviparity in the sebastine scorpaenids may involve egg size and, therefore, gestation time. Egg size in *Helicolenus* is relatively small but gestation time is unknown (Graham, 1939). *Sebasticus*, a relatively primitive genus, has a shorter gestation time (20–25 days) and larvae are born immediately after hatching from the chorion (Tsukahara, 1962). Larvae at birth are small, near 3.7 mm total length, but are fully developed and ready to commence feeding (Tanaka, 1973). In species of *Sebastes* on the west coast of North America, the egg size is generally 1 mm or less and gestation time is typically intermediate, estimated as 37 days for *S. melanops* (Boehlert & Yoklavich, 1984) and 41.5 days for *S. caurinus* (Dygert, 1986). With a 1.2 mm egg, gestation time in *S. schlegeli* increases to 51.5 days (Fig. 1) and the characteristics of additional nutrition are similarly greater (Figs. 3 and 4; Table I). The longer gestation period may allow more time for absorption of nutrients. Our results suggest that viviparity in this group evolved through a passive strategy as suggested by Wourms (1981).

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ASPECTS OF THE REPRODUCTIVE BIOLOGY, SPATIAL DISTRIBUTION, GROWTH, AND MORTALITY OF THE DEEPWATER CARIDEAN SHRIMP, *HETEROCARPUS LAEVIGATUS*, IN HAWAII

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ABSTRACT

The recent rapid development of fisheries for the *Heterocarpus laevigatus* in Hawaii and elsewhere in the tropical Pacific has created the need for biological information to manage the resource. This study reports on a 16-month sampling program of commercial shrimp catches in Hawaii, during which the depth of capture, carapace length (CL), sex, and reproductive condition of 7,368 *H. laevigatus* were determined.

The overall sex ratio of *H. laevigatus* was 1:1.16 in favor of females and depended on the depth sampled; there were relatively fewer females as depth increased. Seasonal variation in sex ratio was evident which may have been due to changing catchability and availability or a sex related dispersion pattern. Sex ratio also depended on size category, displaying a standard pattern with no evidence of protandry.

Females mature at 40 mm CL (64% of asymptotic length) and ovigerous individuals are found year round. However, the main reproductive season is from August-February, with over 50% of females carrying eggs from October-January. Mature shrimp may undergo a depth related seasonal migration in synchrony with breeding. Mature males and females were found deeper (700 m) during the reproductive season than not (550 m). Females apparently settle in deep water and migrate gradually to shallower water as they grow.

Seasonal length-frequency data suggest *H. laevigatus* is not semelparous. Separate analyses of CL-frequency distributions of male and female shrimp indicate their von Bertalanffy asymptotic sizes are 57.9 and 62.5 mm CL, respectively. Growth coefficients (K) estimated by modal progression were 0.35 and 0.25 per year for males and females, and total instantaneous mortality rates were 1.51 and 0.73 per year, respectively.

The deepwater caridean shrimp, also known as "ono" or smooth nylon shrimp, *Heterocarpus laevigatus*, (Family Pandalidae) occurs throughout the tropical Pacific Ocean, where it is found in benthic deepwater habitats (450-900 m) (Wilder 1977; King 1983). While early trapping surveys in the Hawaiian Islands revealed its local abundance (Clarke 1972; Struhsaker and Aasted 1974), little information was available concerning its biology. These early studies did show, however, that *H. laevigatus* was potentially of commercial importance, with a preliminary maximum sustained yield estimate of 454-907 metric tons (t) derived for the Hawaiian Archipelago (Department of Land and Natural Resources 1979). More recently the Western Pacific Regional Fishery Management Council[3] (WPRFMC) has revised this estimate to 400-4,000 t.

A commercial trap fishery for this species subsequently developed in the Hawaiian Islands, and in 1984 the WPRFMC began the process of developing a fishery management plan for the *Heterocarpus* shrimp resources of the region. Landings from the Hawaiian fishery exceeded 135 t in 1983 but have declined sharply since, although commercial interest in the resource remains great (WPRFMC fn. 3). Recent research surveys in Hawaii have now more clearly defined this species' depth, temporal, and geographic distributions (Oishi 1983; Hawaiian Divers 1983[4]; Gooding 1984), although the life history of *H. laevigatus* remains largely unknown. The only substantive biological studies to date were

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[3] Western Pacific Regional Fishery Management Council. 1984. Status of fisheries assessment of development and management needs for selected crustacean species in the western Pacific region. Unpubl. manuscr., 60 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

[4] Hawaiian Divers. 1983. Deepwater shrimp utilization study for Hawaii. Report prepared under NOAA Cooperative Agreement No. 80-ABH-00065 for the Southwest Region, Western Pacific Program Office, National Marine Fisheries Service, NOAA, Honolulu, HI, 47 p.

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completed in the Marianas (including Guam) and Fiji (Wilder 1977; King 1983; King and Butler 1985; Moffitt and Polovina[5]).

Evidence also exists to show that this species is highly susceptible to trapping (Ralston 1986) and, according to commercial fishermen, depletion of the resource has occurred over certain fishing grounds in Hawaii (S. Barrows[6]). Because estimates of the shrimp's productive capacity which are currently available are preliminary at best and a fishery has developed rapidly, this study set out to examine aspects of the life history of the Hawaiian stock of *H. laevigatus* to obtain information useful in developing a basis for management of the fishery.

METHODS

All sampling was conducted by commercial fishing vessels owned by the Hawaiian Shrimp Company (*Easy Rider*, *Mokihana*, and the *Easy Rider Too*) over the 16-mo period from August 1983 to November 1984. During this time, six 35-60 d cruises were completed and samples were obtained during 9 of the 12 calendar months (Table 1). Fishing was conducted throughout much of the Hawaiian Archipelago, from Gardner Pinnacles south to the Island of Hawaii (Fig. 1). Samples were collected at all of the seven main islands (Hawaii, Kauai, Lanai, Maui, Molokai, Niihau, and Oahu) and from Necker, French Frigate Shoals, and Gardner Pinnacles in the Northwestern Hawaiian Islands.

All shrimp were caught during overnight sets of baited pyramidal traps, which measured 1.5 × 1.8 m with a funnel opening at the top center. Fishing was targeted between depths of 500 and 700 m, although some catches were made in both shallower and deeper water because of the trap drift. The best catch rates were found in areas of hard rough bottom; otherwise, all sampling sites were to all appearances similar.

TABLE 1.—Temporal and geographic distribution of *Heterocarpus laevigatus* samples (FFS = French Frigate Shoals).

Year	Month	Location	Sample size
1983	Aug.	Oahu	79
1983	Sept.	Oahu	26
1983	Oct.	FFS	188
1983	Nov.	FFS	1,942
1984	Jan.	Oahu	285
1984	Mar.	Niihau, Kauai	530
1984	April	Hawaii	631
1984	May	Lanai, Maui, Molokai	1,389
1984	June	Necker	842
1984	Sept.	Gardner Pinnacles, FFS, Necker	1,438
1984	Nov.	Necker	18

Systematic subsamples of the catch were taken from every other trap on every second fishing day by randomly scooping approximately 0.9 kg (2 lb) of shrimp from traps prior to emptying. Samples were placed in double bags with tags recording date, location, depth, and condition, and were then frozen and packed for transfer to the laboratory. There all shrimp were identified to species; sexed; examined for embryos on the pleopods; measured to the nearest 0.1 mm for carapace length (CL), carapace width (CW), and total length (TL); and weighed to the nearest 0.1 g on a top loading scale. The data were then keypunched and stored for analysis.

Size-frequency distributions of *H. laevigatus* were analyzed by the regression method of Wetherall et al. (in press) to estimate maximum size (L_∞ of the von Bertalanffy growth equation) and the ratio of total instantaneous mortality rate (Z) to von Bertalanffy growth coefficient (K). Additionally, the growth coefficient of *H. laevigatus* was estimated by following the progression of size modes evident in three large samples taken: 1) 24 October to 6 November 1983, 2) 24 April to 11 May 1984, and 3) 3 September to 6 November 1984. Sample sizes of N = 2,021, 1,991, and 1,438 were obtained in these respective samples, accounting for 74% of all shrimp measured in the study. Modal progression of size distributions was determined by the ELEFAN I computer program of Pauly (1982).

RESULTS

A total of 7,368 *H. laevigatus* were measured and examined for CL, sex, and the presence of eggs (Table 1). Of these 3,956 were females (32.6% of which were ovigerous) and 3,412 were males. This corresponds to an overall male to female sex ratio of 1:1.16, departing significantly from equality ($P < 0.0001$). Measurements of TL, CW, and weight were obtained from 5,920 of the shrimp sampled.

Due to an imbalance in sampling, the effects of location and time on the distribution of *H. laevigatus* could not be completely separated. We therefore assume that all samples were drawn from statistically homogeneous locations in order to isolate and examine temporal and depth effects. The strength of this assumption is based largely on our personal observations and those of fishermen that seasonal change seems to account for most major population

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[5] Moffitt, R. B., and J. J. Polovina. The distribution and yield assessment of the deepwater shrimp resource in the Marianas. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

[6] S. Barrows, Hawaiian Shrimp Company, 737 Bishop Street, Suite 2910, Honolulu, HI 96813, pers. commun. 1985.

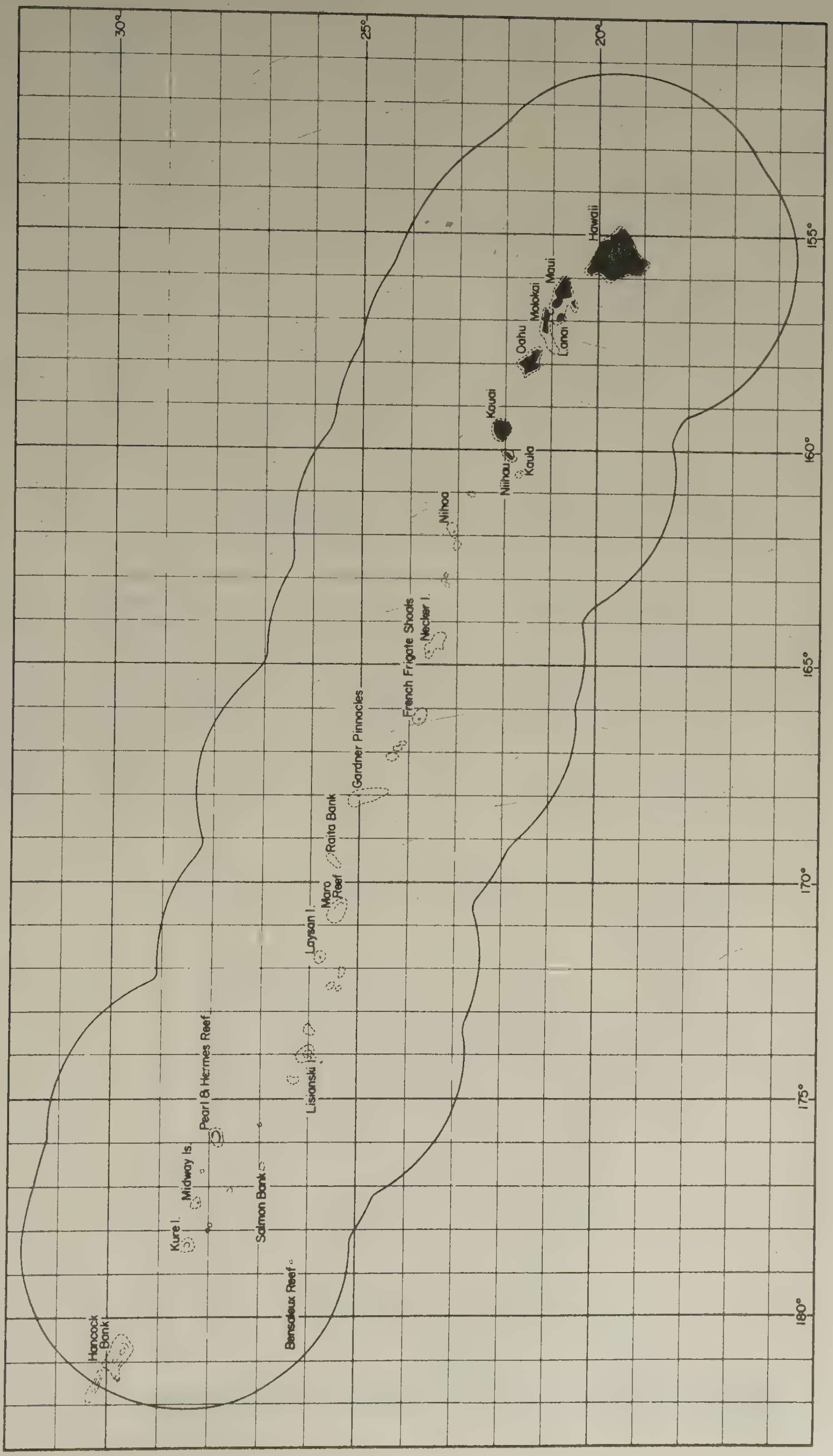
30°
25°
20°
155°
160°
165°
170°
175°
180°
Hawaii
Maui
Molokai
Lanai
Oahu
Kauai
Niihau
Kaula
Nihoa
Necker I.
French Frigate Shoals
Gardner Pinnacles
Raita Bank
Maro Reef
Laysan I.
Lisianski I.
Pearl & Hermes Reef
Midway Is.
Kure I.
Salmon Bank
Bensaleux Reef
Hancock Bank

FIGURE 1.—Map of the Hawaiian Archipelago showing sampling locations. Note that the circumscribed area delimits the U.S. fishery conservation zone and that one degree of latitude equals 111 km.

variations in Hawaii, as well as evidence from the Mariana Archipelago which shows that populations of *H. laevigatus* are affected to a greater degree by temporal factors than geographic ones (Polovina[7]).

Morphometrics

The results of performing functional regressions (Ricker 1973) on the three linear size measurements (CL, CW, TL) are given in Table 2. Estimates of slope and intercept are provided for all possible permutations of these variables. Separate analyses for males (M), females without eggs (F0), and females with eggs (FE) were not performed because all have similar gross morphologies (but see King and Moffitt 1984). As expected, the data were well described with a linear fit.

The relationship between weight and CL was examined by analysis of covariance (BMDP 1977) to determine whether the M, F0, and FE subgroups have different weight-length relationships. Results showed all three were characterized by differing slopes in the regression of $\log_e$ (weight) on $\log_e$ (CL) ($F = 86.46$, df = 2, 5912, $P << 0.0001$). Parameter estimates with standard errors and other regression statistics are presented in Table 3 for each of the three subgroups. Note that the reduced r^2 of the FE group is due to a substantial reduction in the range of CL over which the data were fitted. The results of performing functional regressions of $\log_e$ (weight) on $\log_e$ (CL) are also given.

During the analysis an anomalous bimodal distribution of weight at length emerged. The bimodality was not due to sexual class (M, F0, or FE) and clearly diminished to a unimodal weight distribution as CL increased from 15 to 40 mm. We have no explanation for these data.

Reproductive Biology

The reproductive season of *H. laevigatus* was estimated by plotting the percentage of ovigerous females relative to total females against the month sampled. For the data which overlapped 1983 and 1984 no interannual difference was evident (i.e., the timing of reproduction was similar), so the data were pooled by month between these years. The results are presented in Figure 2 where the data have been further aggregated into 2-mo "seasons". For each the percentage of females bearing eggs is plotted with its 95% confidence interval and associated sample size given above.

The data show an increased incidence of ovigerous females from August to February (>30% of females). In particular over 50% of all sampled females carried eggs from October to January. Relatively few shrimp were caught with eggs during the period from April to July (<10%). Moreover,

TABLE 2.—Parameter estimates of functional regressions on linear size measurements. All measurements in millimeters and all sample sizes n = 5,920.

Dependent variable	Independent variable	Slope	Intercept	Correlation coefficient
Total length	Carapace length	2.864	10.182	0.963
Carapace width	Carapace length	0.613	−5.562	0.964
Carapace length	Total length	0.349	−3.536	0.963
Carapace length	Carapace width	1.630	9.098	0.964
Carapace width	Total length	0.214	−7.737	0.902
Total length	Carapace width	4.673	36.153	0.902

TABLE 3.—Functional and predictive length-weight regressions for *Heterocarpus laevigatus*. The natural logarithm of weight in grams is fitted to the natural logarithm of carapace length in mm. The standard errors of the slope (b) and intercept (a) are given by S_b and S_a respectively.

		Slope	Intercept	S_b	S_a	n	r^2
Males	Predictive	2.755	−6.809	0.0176	0.0629	2,788	0.8976
	Functional	2.910	−7.358	—	—	—	—
Females without eggs	Predictive	2.605	−6.252	0.0185	0.0671	2,202	0.8999
	Functional	2.745	−6.757	—	—	—	—
Females with eggs	Predictive	1.815	−2.986	0.0550	0.2114	928	0.5401
	Functional	2.470	−5.498	—	—	—	—

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[7] J. J. Polovina, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, NI 96822-2396, pers. commun. June 1985.

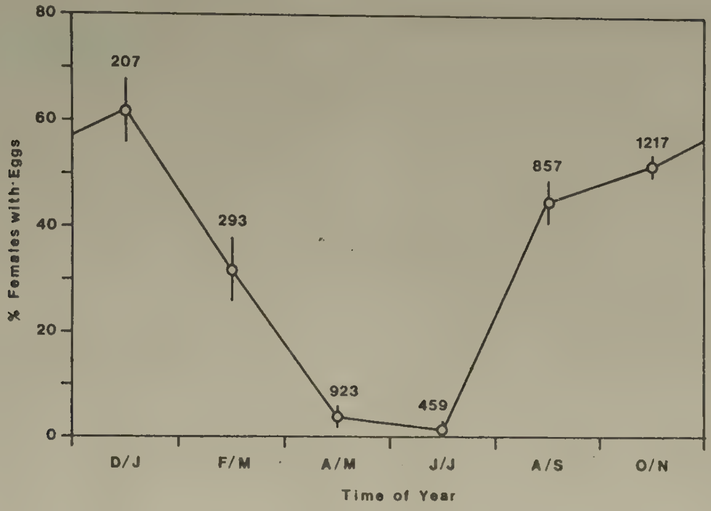

FIGURE 2.—Seasonal incidence of ovigerous *Heterocarpus laevigatus* females in the Hawaiian Islands. Vertical bars represent 95% confidence intervals and sample sizes are presented above. Site locations vary.

when the analysis was restricted to mature females only (see next section) the seasonal pattern of egg-bearing was unchanged. From these results we conclude that in Hawaiian waters *H. laevigatus* reproduces during the fall and winter seasons (August-February).

The size at maturity of female shrimp was determined by aggregating the female data into 5 mm CL classes and plotting the incidence of ovigerous females against CL class (Fig. 3). Only samples obtained during the reproductive season were included in the analysis. As before, the overall percentage

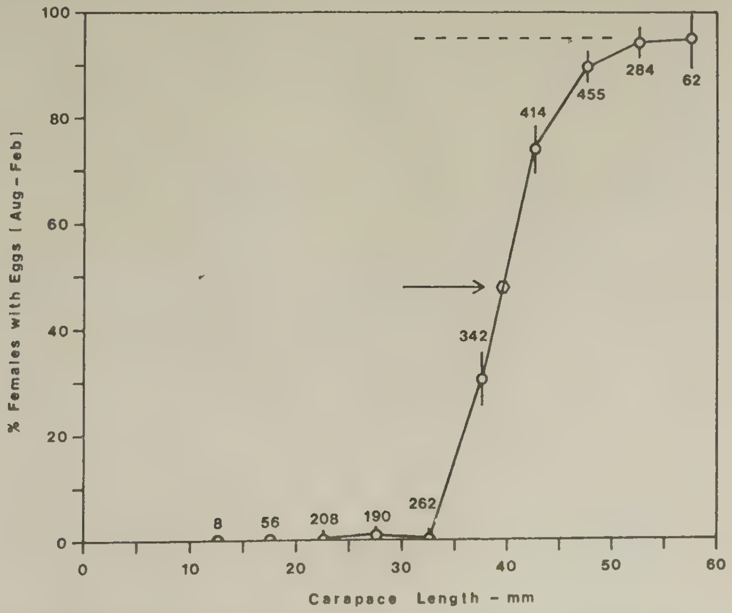

FIGURE 3.—Size at maturity for female *Heterocarpus laevigatus* sampled during the reproductive season. Vertical bars represent 95% confidence intervals and sample sizes are presented above.

with 95% confidence limits and sample sizes are provided.

The data show that the 55-60 mm CL class encompassed the largest shrimp observed. Virtually all (95%) females >50 mm CL that were sampled during August-February bore eggs. Conversely, up to 35 mm CL no more than 1% of the shrimp examined were ovigerous. The figure shows further that at a CL of 40 mm the percentage of ovigerous females is one-half its maximum value, with 48% of all sampled females bearing eggs. We conclude that females become sexually mature at this size (Gunderson et al. 1980). We have no data on maturation in males.

The data presented in Figure 4 show the sex ratio of shrimp as it depends on size (CL mm). Plotted are the percentage females, with 95% confidence intervals and sample sizes, against 5 mm CL size classes. The data clearly show that *H. laevigatus* maintains a relatively uniform sex ratio from 10 to 45 mm CL, but that females predominate in the largest length categories (45-65 mm CL).

Because some studies (Clarke 1972; Wilder 1977) have indicated that *Heterocarpus* females may experience mass mortality after egg bearing, we examined the relationship of sex ratio to season (Table 4). Presented for each 2-mo sampling period are the number of females and total number of shrimp sampled, the proportion which are female, and the standard error of the proportion. The results show that an unusually high fraction (0.72) of the shrimp sampled during the peak of the reproductive season (December-January) are female. Note that the incidence of females in trap samples declines significantly to a value of 0.45 in April-May as the breeding season wanes. At first inspection these data support the contention that females experience increased mortality after bearing eggs, i.e., that *H. laevigatus* may be semelparous.

TABLE 4.—Sex ratio of *Heterocarpus laevigatus* by month sampled. The standard error of the proportion is given by S_p.

Month	Number of females	Proportion of females	n	S_p
December-January	207	0.72	285	0.026
February-March	293	0.55	530	0.022
April-May	923	0.45	2,020	0.011
June-July	459	0.54	842	0.017
August-September	857	0.55	1,542	0.013
October-November	1,217	0.56	2,148	0.011

Spatial Distribution

The relationship between the sex ratio of *H. laevigatus* and sampling depth is provided in Table 5. These results demonstrate that the relative abundance of the two sexes is not independent of depth ($\chi^2 = 165.6$, df = 16, $P < 0.001$). As depth increases (440-760 m) there is a significant decline in the percentage of females in our samples ($P = 0.05$).

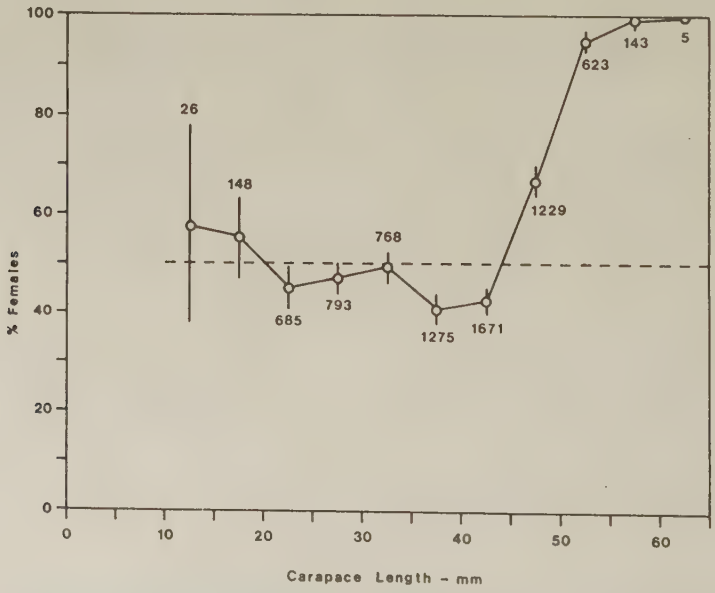

FIGURE 4.—Sex ratio as a function of carapace length. Vertical bars represent 95% confidence intervals and sample sizes are presented above.

TABLE 5.—Sex ratio and size of *Heterocarpus laevigatus* by depth (M is for males, F0 for females without eggs, and FE for females with eggs). S_p is the standard error of the proportion.

Depth (m)	Number of females	*N*	Proportion of females	S_p	Carapace length			
					All	M	F0	FE
440	41	71	0.58	0.059	40	34	43	48
60	9	11	0.81	0.116	39	36	40	—
80	65	141	0.46	0.042	38	33	42	49
500	155	230	0.67	0.031	42	34	45	49
20	287	430	0.66	0.023	43	40	45	46
40	419	943	0.44	0.016	37	35	40	49
60	193	487	0.39	0.022	37	36	38	45
80	280	500	0.56	0.022	39	35	42	47
600	282	498	0.56	0.022	38	35	38	46
20	284	463	0.61	0.023	39	35	34	48
40	325	581	0.55	0.021	38	37	32	47
60	109	210	0.51	0.034	37	34	35	44
80	95	167	0.56	0.038	39	37	35	48
700	90	222	0.40	0.033	36	36	31	43
20	399	738	0.54	0.018	39	38	32	47
40	68	126	0.53	0.044	40	37	33	48
60	14	46	0.30	0.068	34	34	28	42

The results presented in Table 5 also show the distribution of mean size (CL mm) by depth (m) for all *H. laevigatus* caught, and for the M, F0, and FE subgroups. For all shrimp combined, average size decreases slightly with increasing depth fished. The trend for decrease in size with increasing depth is not evident in the M subgroup. However, the F0 class demonstrates a strong relationship of decreasing mean CL with depth. For the FE category the decline is much less apparent, if at all. Thus the overall decline in mean CL of all shrimp combined, is clearly due to an overriding influence of females without eggs. We interpret these trends, or lack thereof, to indicate that young (i.e., small) females may move from deep to shallow water as they mature.

There is some evidence that the depth distribution of *H. laevigatus* changes with reproductive activity (i.e, season). Figure 5 presents the depth distributions for reproductively competent (>40 mm CL) male and female shrimp, classified into samples taken outside (March-July) and during the reproductive season (August-February). Note that depth distributions of both male and female shrimp are

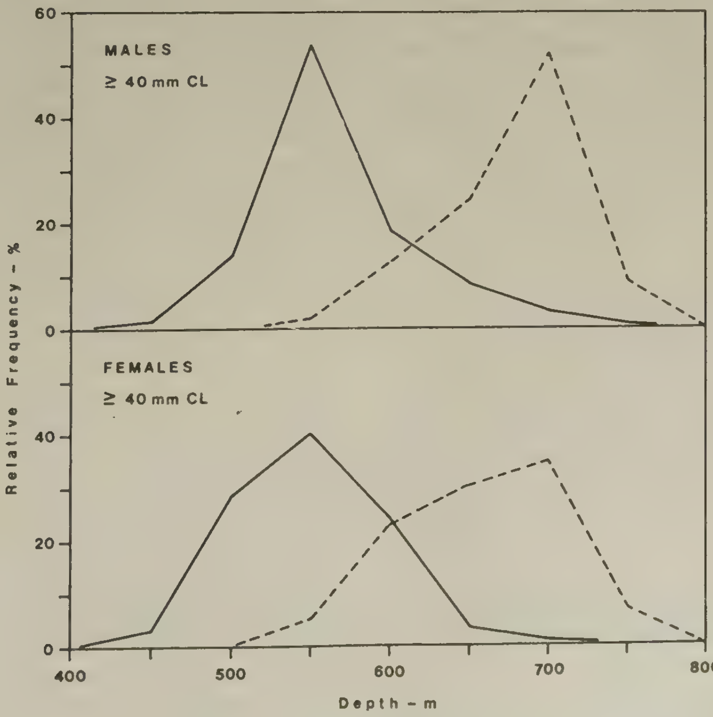

FIGURE 5.—Seasonal distributions of large (>40 mm) male and female *Heterocarpus laevigatus* by depth. The dashed line represents the spawning season distribution (May-February) and the solid line represents the distribution during the nonspawning season (March-July).

shifted 150 m deeper when the females are ovigerous. Although the data are not corrected for what may have been differences in fishing effort by depth, it is true that fishing was targeted to depths of maximum shrimp abundance. Based on these findings, and the results presented in Table 5, our data are consistent with a hypothesis of gradual movement of small females from deep to shallow water, with mature shrimp moving between depths of 550 and 700 m in synchrony with the ovigerous cycle of females.

Growth and Mortality

Clarke (1972) and King (1983) have suggested that *Heterocarpus* spp. may breed once and die. Indeed the results already presented in Table 4 may be considered consistent with the hypothesis that at least female *H. laevigatus* are semelparous. To further address this question we examined the size structure of male and female shrimp classified as follows: 1) during the latter half of the reproductive season (January-February) and 2) immediately following the reproductive season (March-July). If postreproductive mortality of shrimp was severe, a decrease in the relative abundance of large, breeding adults would be expected as the reproductive season waned.

The results presented in Figure 6 conflict with this expectation, where it is apparent that the proportional representation of large reproductive individuals (>40 mm CL) is actually greater imme-

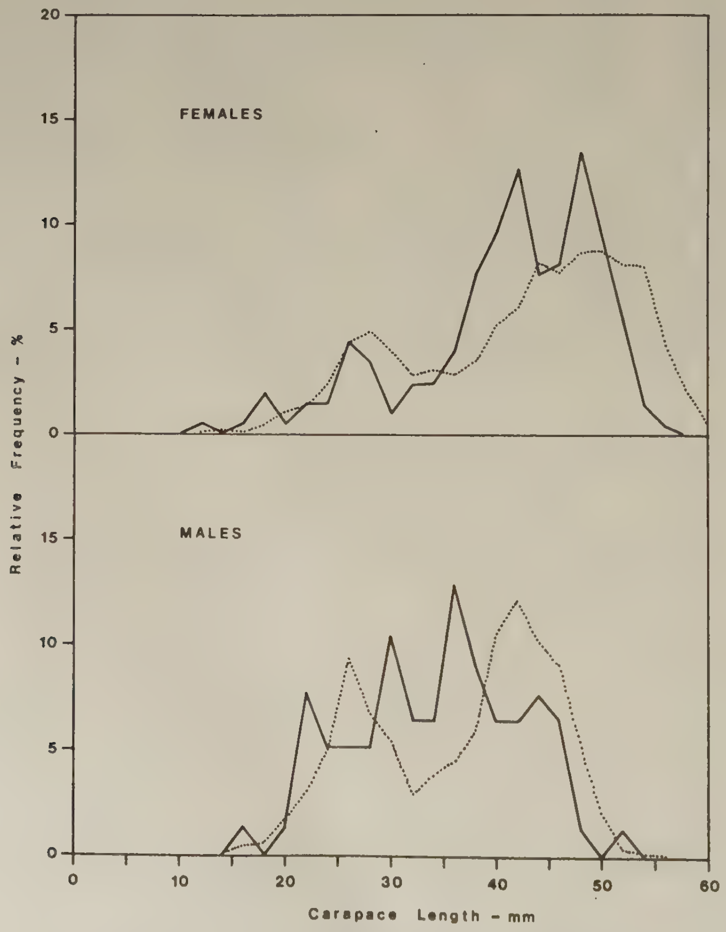

FIGURE 6.—Relative size-frequency distributions of male and female *Heterocarpus laevigatus* during the peak and postreproductive seasons. The solid line represents the peak season (January-February), males N = 78, females N = 207; the dashed line is based on data collected immediately after the peak season (March-July) males N = 1,717, females N = 1,675.

diately following than during the latter half of the reproductive season.

The total sample CL-frequency distribution of males and females combined was analyzed by the regression method of Wetherall et al. (in press) to estimate L_∞ and Z/K. When all shrimp are pooled (N = 7,368), an estimate of L_∞ = 61.7 mm CL results. Further, the ratio of total mortality rate to von Bertalanffy growth coefficient (Z/K) is estimated to be 2.6. Calculations were repeated for separate male and female subgroups, where it was found that L_∞ = 57.9 and 62.5 mm CL and Z/K = 4.3 and 2.9 for males and females, respectively. These results indicate that males generally grow to a smaller size than females.

The results of analyzing the progression of CL size modes in frequency distributions of male and female *H. laevigatus* provided preliminary estimates of K = 0.35 yr^{-1} for males and 0.25 yr^{-1} for females. The former result must be viewed with caution, however, because two "solutions" were detected by the computer search algorithm (Pauly 1982) which differed little in fit. One of these, K = 0.70 yr^{-1}, we believe to be unjustifiably high in light of the minor difference (8%) between the L_∞ of males and the L_∞ of females obtained from the regression analysis. Note that estimates of K and L_∞ typically show a strong inverse correlation (Gallucci and Quinn 1979). These results, in conjunction with the estimates of Z/K for male and female shrimp presented earlier, provide the basis for preliminary estimation of total mortality rate. We estimate Z = 1.51 yr^{-1} for males and 0.73 yr^{-1} for females, corresponding to annual survivorship fractions of 22% and 48% per year, respectively. These data indicate that males grow faster while experiencing a substantially greater total mortality rate than females.

DISCUSSION

Earlier it was assumed that, aside from depth, all shrimp samples were drawn from locations which are dynamically homogeneous; i.e., the behavior of shrimp populations through time does not vary from site to site. This is clearly a restrictive and simplifying assumption and is without doubt the major limitation on the results presented here. Nonetheless, it was a necessary simplification for us to analyze the commercial fishing data upon which this study was based. Consequently, we view those results which rely upon this assumption as tentative and in need for further validation.

Examination of the seasonal trend in the relative abundance of ovigerous females showed that in Hawaii over 50% of *H. laevigatus* females bear eggs from October to January, with a peak between August and February. Wilder (1977) found a similarly timed but more narrowly defined breeding season for *H. laevigatus* in Guam, where the percentage of ovigerous females in trap catches reached a maximum during December, but was not particularly high in any other month. Clarke (1972) reported that *H. ensifer* in Hawaii also reproduces in the winter. The breeding season of these shrimps is unusual among Hawaiian crustaceans and fishes, which typically reproduce during the spring and summer and uncommonly during the winter (Watson and Leis 1974; Lobel 1978; Uchida et al. 1980; Uchida and Tagami 1984; Walsh 1984).

Our data also indicate that in Hawaii sexual maturity of female ono shrimp occurs at approximately 40 mm CL, a size similar to that reported by King (1983) for shrimp from Fiji, Vanuatu, West Samoa, and Tonga and by Moffitt and Polovina (fn. 5) for samples from the Marianas. Based upon the estimated parameters of the von Bertalanffy growth equation derived here, this corresponds to an age of first maturity of 4 yr. Although we have no data on the maturation of males, we believe they probably mature earlier and at smaller size, perhaps at age 3 when they are 37-38 mm CL. Such a result is consistent with the findings of Moffitt and Polovina (fn. 5) who found that male *H. laevigatus* in the Marianas mature at a smaller size than do females.

Wilder (1977) speculated that both *H. ensifer* and *H. laevigatus* in Guam are protandrous hermaphrodites, as did Clarke (1972) for Hawaiian populations of *H. ensifer*. However, the results presented in King and Moffitt (1984) tend to contradict this conclusion. These authors studied the morphometry and sexuality of five deepwater pandalids, including *H. laevigatus*, in Fiji and the Marianas. Using the relative length of the appendix masculina expressed as a proportion of CL, they found no tendency toward protandrous hermaphroditism. Moreover, the sex ratio reported in their study was approximately 1:1.

Our results also indicate that for Hawaiian populations of *H. laevigatus*, and we speculate for most tropical pandalids, a sex transition does not occur. Wenner (1972) has termed the pattern exhibited in Figure 4 the standard sex ratio pattern, as distinguished from one of reversal. Due to the large numbers of females in small size classes, these data are generally inconsistent with a protandric hermaphroditic life history, as has been hypothesized by previous workers on *Heterocarpus* spp. (Clarke

1972; Wilder 1977). King and Moffitt (1984) also argue for dioecy in this species based upon relative changes in the morphology of the appendix masculina.

Evidence now exists to suggest that the sex ratio of *H. laevigatus* undergoes a seasonal change (Table 4), although the reasons for this are at present unknown. A biological alteration in population structure of this order seems unlikely. Rather, the relatively high catch of females during the December-January period may be due to seasonal changes in catchability or vulnerability of one or both sexes to the traps. Alternatively, the spatial dispersion of *H. laevigatus* may depend on sex. If males and females are spatially segregated, the high proportion of females in the December-January sample may have been due to small sample size ($N = 207$).

We have also shown that sex ratio depends strongly on the depth sampled (Table 5), with diminishing representation of females as depth increases. This spatial heterogeneity between the sexes may be due to directed movements. Based on size trends of females we conclude that they recruit to deeper water and subsequently migrate to shallower water. We have no evidence for similar movement of males.

Studies by King (1983) on Pacific *Heterocarpus* spp. showed cyclic migrations in these shrimps, suggesting that depth distribution may change seasonally, with an annual migration up and down the slope of the sea floor. The data presented in Figure 5 indicate that mature *H. laevigatus* in Hawaii do migrate seasonally, demonstrating distinct shifts in the depth distributions of both sexes during the reproductive season. Because this result is confounded by what may be a location effect, however, we view them as preliminary and in need of further confirmation. King (1983) also reported that *Heterocarpus* spp. were found in stomachs of tuna in Fiji, indicating perhaps some type of vertical migration in the water column.

King (1985), based on work completed in Fiji, examined the question of iteroparity and semelparity in several genera of pandalid shrimp (*Plesionika*, *Saron*, *Parapandalus*, and *Heterocarpus*). Based on the difference between length at sexual maturity and maximum length, he concluded that shallow-water species (e.g., *H. ensifer*) are semelparous. He states that deepwater *Heterocarpus* spp. "have an extended reproductive lifespan, the length of which may be taken to indicate the number of spawnings." We conclude, based on the relative size-frequency distributions of males and females during peak and postreproductive seasons, that both sexes survive well after reproducing—evidence in favor of iteroparity. Although a high mortality of shrimp following the breeding season would be evidence consistent with a semelparous life history, it is not a sufficient result to prove it. This is because each female, before dying, could have sequential multiple clutches during the October-February ovigerous period. Nonetheless, good survival of *H. laevigatus* females after carrying eggs (Fig. 6) is indicative of iteroparous reproduction.

The regression technique of Wetherall et al. (in press) produced estimates of the ratio of mortality to growth coefficient of 2.9 and 4.3 for females and males respectively. Moffitt and Polovina (fn. 5), using similar methods, estimated $L_\infty = 55.2$ mm CL and $Z/K = 2.5$ for combined male and female samples of *H. laevigatus* from essentially unfished stocks in Guam and the Marianas. Ralston (1986) also reported that the Z/K ratio of an unexploited population of *H. laevigatus* at Alamagan in the Marianas was about 2.0. The differences between estimates may therefore relate to differences in levels of exploitation. Moreover, the higher mortality rate of male shrimp when compared with females (1.51 versus 0.73 yr^{-1}) may explain the somewhat biased sex ratio in favor of females.

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7.

Conflicts between marine mammals and fisheries off the coast of California

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D. DeMaster, D. Miller, J. R. Henderson and J. M. Coe

Introduction

Marine mammal–fishery interactions can result in both revenue losses to fishermen and mortality of marine mammals. These interactions can involve damage to captured fish, damage to nets and gear, reduced catch rates due to scaring of target species, reduced availability of target species, and incidental entanglement. The purpose of this chapter is to describe two research projects that have been supported by the National Marine Fisheries Service to document the nature and extent of marine mammal–fishery interactions in California. The first project was contracted out to the California Department of Fish and Game, and was directed by Dan Miller (California Fish & Game, Monterey office). The second project is part of the research programme of the Coastal Marine Mammal Project (Southwest Fisheries Center, La Jolla, California). This study, the cooperative Marine Mammal Salvage Program, was originally headed by John Hendersen, and is currently directed by Larry Hansen.

Marine mammal–fisheries interaction study

Beginning in July 1979, the Southwest Fisheries Center and the Southwest Regional Office of the National Marine Fisheries Service jointly sponsored a contract with the California Department of Fish and Game to determine the nature and extent of interactions between marine mammals and all commercial and recreational fisheries in California. The results of the first year of this study are summarised in an annual report (Miller 1981), and a summary of its first two years is given Miller *et al.* (1982) and Herder (1982).

In this contract, an effort was made to determine the loss of fish and damage to gear due to marine mammals by questioning fishermen who had recently completed trips and by sending out observers on fishing trips when possible. In addition, an effort was made to monitor the incidental take of marine mammals in various fisheries. Miller (1981) reported that there was considerable concern on the part of the gill-net and trammel-net fishermen and salmon trollers that information on incidental take of marine mammals may eventually curtail their operations. Estimates of fish loss and gear damage were generally available for all fisheries, whereas estimates of marine mammal take were not available for most fisheries.

Seven fisheries were identified in which a consistent loss of fish and/or damage to gear was occurring (Table 7.1): the commercial salmon trolling fishery, the California

Table 7.1 The value of fish and gear depredated by marine mammals annually (data from Miller *et al.* 1982).

Fishery	Fish lost ($)	Gear lost ($)	Total ($)
Salmon fisheries			
commercial troll	274 000	12 220	286 220
commercial sport boat	6 000	360	6 360
skiff	2 300	0	2 300
Klamath River – subsistence	74 000	10 000	84 000
Total salmon	365 300	22 580	378 880
sport boat non-salmon	27 000	10 730	37 730
Pacific herring	57 100	4 550	61 650
Gill-net	63 360	57 070	120 430
Total fisheries	503 760	94 930	598 690

halibut gill-net fishery, the Native American gill-net fishery in the Klamath River, the commercial sport-boat fishery out of San Diego, the Pacific herring fishery, the partyboat and skiff salmon fisheries, and the round-haul fisheries for anchovy and mackerel. In addition interactions between the southern California squid fishery and California sea-lions and short-finned pilot whales were described (Miller *et al.* 1982), but financial losses were not quantified. Significant interactions with marine mammals were not observed in the following fisheries: the pier fishery, the shoreline hook-and-line sport fishery, the bottomfish skiff fishery, the partyboat bottom-fish fishery north of Morro Bay, the lamprey fishery of the Eel and Klamath rivers, the night and surf smelt fisheries, the bottom-trawl fishery, the lobster fishery, and the swordfish spearing fishery.

The largest financial loss due to interactions with marine mammals was reported from the commercial salmon trolling fishery. A minimum loss of $130 000 during the month of May 1980 was estimated. This estimate does not include losses due to gear damage. The total value of salmon landed in California during May was about $5 000 000. Miller *et al.* (1982) reported that roughly two-thirds of the total value of fish and gear lost due to marine mammals occurred in this fishery (Table 7.1).

The marine mammal species primarily involved in the salmon fishery interactions is the California sea-lion (*Zalophus californianus*). During the 113 observed trips made in 1979–80, only one sea-lion was shot at. Miller (1981) reported that more animals were probably taken in 1979 than are indicated by this one observation. The annual loss of salmon from the recreational catch and from the skiff fishery was much less than for the ocean salmon fishery (Table 7.1).

Miller (1981) reported that the Klamath River Native American (subsistence) gill-net fishery was the most difficult fishery to monitor. He also reported that this is the fishery that is thought to be most affected by marine mammal predation. Harbour seals (*Phoca vitulina*) have been observed to remove netted salmon quickly from the nets (Miller 1981). Entanglement of harbour seals in nets was observed, as well as harbour seals and California sea-lions being shot near the nets (Miller 1981). Herder (1982) reported that roughly 926 salmonids were damaged out of a total harvest of 6800

(14%). If fishermen were to replace these with market fish, this would represent a total loss of roughly $84 000, or $2400 per fisherman.

Losses to marine mammals from the commercial sport-boat fishery were negligible in central California, roughly 2.5% of the total catch in southern California, and over 6% in Baja California (Miller 1981). This loss was primarily due to predation by California sea-lions. The estimated losses computed from definite loss values varied between 15 141 fish and 18 272 fish (Miller *et al.* 1982). Pacific bonito was the most frequently lost fish. Other fish lost included: Pacific mackerel, kelp bass, California barracuda, and several species of rockfish. The value of fish and gear loss in southern California varied between $37 000 and $38 800.

The gill-net and trammel-net ocean fisheries were also significantly impacted by marine mammal predation. In waters off Baja California, 12.5% of the catch was lost to sea-lion predation (Miller 1981). In southern California waters, the estimated fish loss was 2.2%; most of this loss was due to California sea-lions. Losses occurred in the following fisheries (Miller *et al.* 1982): shark drift gill-net fishery ($1400), California halibut gill-net and trammel-net fishery ($72 700; depredation rate of 10.1%), white seabass gill-net fishery ($7980; depredation rate of 10.4%), rockfish set-gill-net fishery ($18 060; depredation rate of 1.6%), white croaker gill-net fishery ($3978; depredation rate of 7.1%), and Pacific bonito gill-net fishery ($1652; depredation rate of 6.5%).

The Pacific herring fishery was difficult to monitor because nets are fished both day and night and are often left unattended. Both California sea-lions and harbour seals have been observed foraging on netted fish. In this fishery, damage to the gear (the nets) may be more significant than loss of fish. Three different types of nets are used in this fishery: gill-nets, lampara nets, and purse-seine nets. Fishermen in this fishery are more concerned with sea-lions frightening fish out of the nets than they are with the actual number of fish eaten by sea-lions that enter nets (Miller *et al.* 1982).

The dip-net squid fishery of southern California was estimated to have lost over $36 000 due to interactions with California sea-lions and short-finned pilot whales (*Globicephala macrorhynchus*) in 1980 (Miller 1981). Fish in the catch are not eaten, but the frightening of squid away from the dip-net area results in a considerably lower catch per unit effort. The squid fishery in Monterey primarily uses lampara nets, and

Table 7.2 Comparison of percentage of catch lost to marine mammal predation from interviews with fishermen and from observed trips at sea. (Figures in parentheses indicate numbers of fish.)

	Data source	
Fishery	At sea (%)	Interviews (%)
commercial salmon (ocean)	2.4 (113)	3.2 (1506)
partyboat salmon	0.64 (72)	1.35 (157)
partyboat salmon	0.0 (13)	0.0 (20)
partyboat bottomfish		
gill-net and trammel-net (bottomfish)		
southern California	0.7 (35)	2.2 (125)
central California	0.0 (5)	2.4 (13)

interaction with marine mammals is relatively rare. The potential for frightening off fish and foraging by marine mammals in the round-haul net fishery for anchovy and mackerel was reported to be high. Data are currently not available on the value of the fish lost, but efforts are underway to determine this.

Miller (1981) provided information on fishery–marine mammal conflicts from at-sea trips and from interviews. A comparison of these techniques is currently underway. However, a preliminary comparison of these two data sets indicates that data from interviews will generally give higher estimates of fish lost to marine mammals than will data from at-sea trips (Table 7.2). Subsequent analyses will need to identify factors that may be contributing to differences between these two sampling techniques. One interpretation of these results is that fishermen overestimate the loss of fish due to marine mammal predation. An alternative hypothesis is that fishermen may be fishing differently when observers are on board. Obviously, many other hypotheses can be generated, and more information is needed to test any of them.

Marine mammal mortality in California fisheries

Miller *et al.* (1982) estimated that 300 California sea-lions were taken each year by shooting in the commercial salmon trolling fishery (Table 7.3). This was determined by interviewing fishermen. There were no reported mortalities of marine mammals associated with the commercial salmon sport-boat fishery, the recreational skiff fishery for salmon, the non-salmon commercial sport-boat fishery, or the Pacific herring fishery. In the shark drift-gill-net fishery, 49 California sea-lions were entangled in 177 at-sea days sampled (Miller *et al.* 1982). This represents a mean catch rate of 0.28 ±0.19 California sea-lions per net-night. Other marine mammals 'taken' included two short-finned pilot whales, three grey whales (*Eschrichtius robustus*), and one baleen whale, but the interaction rates were too low to quantify. Miller *et al.* (1982) estimated that between 678 and 1227 sea-lions were drowned between September 1980 and September 1981 in shark drift gill-nets. Mortality was also reported in the shark set-gill-net fishery and the California halibut gill-net and trammel-net fishery. No mortality was observed in the white sea bass, rockfish, white croaker, California barracuda, Pacific bonito, or flyingfish fisheries (Miller *et al.* 1982), but a few entanglements were reported by fishermen.

In the Monterey Bay halibut gill-net fishery, the estimated marine mammal mortality in June 1980 was 45 California sea-lions, 15 harbour seals, and 15 harbour porpoise (*Phocoena phocoena*). These numbers were determined after 25 days of at-sea observations. No additional marine mammal mortality was reported for the rest of the year (20 observer-days reported by Miller *et al.* 1982). In June 1981, Miller *et al.* (1982) estimated mortalities of 22 harbour seals and 22 California sea-lions. The pinnipeds in 1980 and 1981 were juveniles (Miller *et al.* 1982). In May of 1982, this fishery moved north into Bolinas Bay. D. G. Ainley *et al.* (personal communication) reported that a large number of birds, 13 harbour porpoise and 15 harbour seals were found along a 40-mile stretch of coast. Of the 13 harbour porpoises found, 7 were 'fresh'; 4 had obviously been captured in nets. Historically, the number of stranded harbour porpoises averages 2.1 animals per year, a much lower rate. Additional studies are currently being planned to determine the seasonality of marine mammal mortality due to this fishery, and to assess future trends.

Miller *et al.* (1982) estimated that 10 sea-lions and as many as 30 pilot whales are

Table 7.3 The estimated marine mammal mortality in California fisheries for 1980 (data from Miller *et al.* 1982 and D. G. Ainley *et al.* personal communication).

Species	Fishery	Number
California sea-lions	commercial salmon trolling	300
	Klamath River gill-net	7[a]
	ocean gill-net + trammel-net	1209
	squid round-haul net	10
	anchovy-mackerel round haul	20
	trawl fishery	25
		1571
harbour seal	Klamath River gill-net	22[a]
	ocean gill-net	95
	in-shore gill-net	15[a]
		132
elephant seal	ocean gill-net	**25**
harbour porpoise	ocean gill-net	15
	in-shore gill-net	13[a]
		28
pilot whales	squid round-haul nets	30
	ocean gill-nets	30
		60
grey whale	ocean gill-net	**3**
baleen whale	ocean gill-net	**1**
total all fisheries		**1820**

[a] Actual count, total not estimated.

taken in the squid round-haul fishery in southern California (see Table 7.3). These estimates are based on limited information, as very few at-sea trips were made available by the fishermen. Sea-lions and pilot whales are shot at by fishermen in the squid dip-net fishery, but mortality is thought to be minimal.

In round-haul net fisheries for anchovy and mackerel, Miller *et al.* (1982) estimated that 20 California sea-lions were drowned per year. They also speculated that pilot whales may be taken in this fishery, but thought it likely that pilot whale mortality would be more common in the squid round-haul net fishery.

Finally, Miller *et al.* (1982) reported that a small number of sea-lions (see Table 7.3) are drowned by entering operating trawl nets; most have been drowned, but some lived and were returned to the water. Sea-lions are known to follow trawl nets and feed on smaller fishes passing through the webbing.

The impact of the incidental mortality presented in Table 7.3 is difficult to predict and will only be briefly discussed. Population estimates are only roughly known for some of the impacted species (Table 7.4). Relative to their maximum *per capita* growth rate, only the incidental take of California sea-lions and short-finned pilot whales is

Table 7.4 Estimated population size and percentage fishery-related mortality rate for marine mammals that occur off the coast of California.

Species	Population	Mortality from fisheries (%)	References
California sea-lion[a]	45 000 – 60 000	3–4	Le Boeuf and Bonnell (1980)
Pacific harbour seal			
Oregan border to Pt Conception	17 000		Miller *et al.* (1982)
Channel Islands	3 000	<1	Stewart and Yochem (1982)[1]
	20 000		
northern elephant seal	60 000 – 90 000	<1	Le Boeuf and Bonnell (1980)
harbour porpoise[b]			
short-finned pilot whales[b]	400 – 2 000	3–15	Dohl (1980), Stewart and Yochem (1982)
grey whale	16 000	<1	Reilly (1981)

[a] US population only.
[b] California population.

significant. More information on the population size of harbour porpoise is needed to determine the significance of the observed level of take. In all cases where incidental take occurs, the age and sex composition of the take is unknown.

Coastal marine mammal salvage programme

Additional information on marine mammal–fisheries interactions can be collected via salvage of beached marine mammals. In 1979, the Southwest Fisheries Center (SWFC) initiated a co-operative programme among San Diego area researchers to inspect and salvage stranded marine mammals from beaches in San Diego County. Dead marine mammals are recovered routinely in this programme by staff of the Coastal Marine Mammal Project, SWFC. In addition to collecting basic data (species, sex, morphometrics, photographs) from each stranding, the staff also thoroughly inspects each carcass for external wounds or trauma which might be human related. Carcasses which are judged not excessively decomposed (usually having been dead less than approximately 48 hours) are collected intact and subsequently undergo a thorough necropsy by a marine mammal veterinarian.

Events leading to traumatic death of marine mammals may, but will not always, result in a carcass exhibiting injuries, wounds, or other obvious signs of the cause of death. Gunshot wounds are usually readily detectable even in decayed carcasses. Because of firearm restrictions on virtually all beaches in San Diego County, shooting of already beached dead animals seldom occurs, hence any bullet wound is likely to have been incurred while the animal was alive. Cetaceans which are found with severed flukes and missing terminal vertebrae can generally be assumed to have been entangled in a net, though it is not evident whether these animals died as a direct result of the injury or suffocated in a net and were subsequently cut loose. Live, 'tailless' whales, both grey whales (*Eschrichtius robustus*) and short-finned pilot whales, have been observed in southern California. Suffocation resulting from entanglement in a net results in tissue damage which is difficult to detect, and evidence for suffocation is often circumstantial. The presence of gastric contents and vomitus in the oesophagus, and froth or foam in the trachea suggests suffocation. The presence of food in the stomach generally indicates some form of sudden, untimely death, as chronically ill marine mammals which strand generally have empty stomachs.

In 1980, 16% (3 of 19) of the recovered sea-lions showed evidence of human-related mortality; all four of the salvaged pilot whales showed evidence of fishery interactions. In 1981, 34 marine mammal specimens were fresh enough to autopsy; all but four of these were sea-lions. Gunshot wounds were the most common cause of death (37%). The next most frequent cause was hypoglycemia (18%; Hansen 1981). We hope that the data collected from this type of research will provide enough information to ascertain what proportion of the total mortality is due to human activities, including commercial and recreational fisheries.

Conclusion

A financial loss of approximately $600 000 per year was found to be related to marine mammal–fishery interactions in California. Over half of this loss was from salmon fisheries. This represents damage to the catch and to gear, and does not include losses due to frightening of fish from nets or from reducing the availability of target species. The incidental mortality of marine mammals is roughly 1800 animals per year. Though not known precisely, the *per capita* mortality rate due to fishery interactions is probably only significant for California sea-lions and short-finned pilot whales. Without information on stock discreteness and the age–sex composition of the take, it is not possible to determine the impact of fishery-related mortality on any of the populations involved. Because of problems relating to placing observers on commercial fishing boats, the age–sex composition of animals caught incidental to commercial fishery activities will have to be inferred from salvaged marine mammals. Studies directed at monitoring population trends of impacted species will have to be continued to ensure that this type of human activity does not adversely affect any of the stocks of marine mammals that occur off the coast of California. Studies directed at mediating losses to fishermen are currently underway by both the California Department of Fish and Game and the National Marine Fisheries Service.

Acknowledgements

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LUTJANIDAE

Ehu

by Alan R. Everson

Valid name	*Etelis carbunculus* Cuvier 1828 (Fig. 61)
Synonymy	*Eteliscus marshi* Jenkins 1903
	Etelis marshi Jordan and Evermann 1905
Common and vernacular names	Red snapper; Marsh's snapper; squirrelfish snapper; ulaula; ehu

Distribution

Found around every major island and bank in the Hawaiian Islands and in the NWHI from Nihoa to Kure Atoll at depths ranging from 102 to 271 m.

Distinguishing characteristics

D. X, 11; A. III, 8; P1. 16; Gr. 6+12 (Jordan and Evermann 1905). Interorbital region flattened; maxilla with scales; dorsal fin continuous, but spinous portion of fin incised at its junction with soft portion; dorsal and anal fins without scales; ultimate dorsal and anal soft rays longer than penultimate soft rays (Anderson 1981).

Mouth rather large, somewhat oblique. Teeth on vomer and palatine. Teeth on the jaws in villiform bands; outer series of enlarged, widely spaced canines in each jaw; longest in front on each side; thicker in the upper jaw than lower. Body color uniform rose red in life (Jordan and Evermann 1905).

Ehu is sometimes confused with its congener, *E. coruscans*. It can be separated by the following features: horizontal yellow band along the middle of sides on ehu, absent on onaga; red coloration on inside of mouth lacking in ehu; long caudal rays on onaga; ehu is more robust and has fewer gill rakers than onaga (Jordan and Evermann 1905).

Life history

Ehu attains sexual maturity at about 29.8 cm FL. A fish, 50.8 cm FL, releases over 1.3 million eggs per batch and may release 2 or more batches of eggs per spawning season which extends from May through October (Everson 1984).

Because ehu are caught at considerable depths, the ascent causes the gas bladder to expand, thus forcing the stomach to evert. Therefore only a small number of stomach content samples was collected. Based on the number of small fishes and crustaceans found in stomachs, ehu is a carnivorous bottom feeder.[17]

Daily rings on the sagittae of ehu were used to estimate age and growth rate. The von Bertalanffy growth model for this species is:

$$L_t = 63.9\ (1 - e^{-0.36(t-0.60)}),$$

where L = fork length (cm) expressed as a function of time t in years (see footnote 10). From this equation, ehu is estimated to be 28.4 cm at 1 year, 39.2 cm at 2 years, and 46.8 cm at 3 years.

The functional length-weight relationship of 754 ehu 26.8 to 63.5 cm long is:

$$W = 1.13 \times 10^{-8}\ L^{3.0740},$$

where W = weight (kg) and L = fork length (mm) (Uchiyama et al. 1984).

The NMFS catch data showed that ehu is the dominant species at banks west of Lisianski; ehu represents 22.7 to 86.5% of the catch (Uchiyama and Tagami 1984). In comparing mean lengths of ehu among banks of the NWHI, fish is larger west of Lisianski Island (Uchiyama et al. 1984). The relative apparent abundance of ehu is higher west of Lisianski Island; the catch rate was 4.1 fish per line hour at Nero Seamount (Uchiyama and Tagami 1984). Similar trends were also noted by Moffitt (1980). The sex ratio of ehu from the NMFS data is 67:33 (N = 926) in favor of females. The mean weight of females (2.13 kg) is somewhat greater than that of males (1.56 kg); however, the difference is not statistically significant (Uchiyama et al. 1984).

Gear and catch

Ehu is traditionally caught with deep-sea handlines, but it can also be trapped. In Hawaii, it is an important commercial species (Uchida et al. 1979). From 1961 through 1971, the annual catch fluctuated between 5,800 and 12,700 kg; however, during 1972-79 landings increased, ranging from 9,900 to 16,200 kg per year. The average annual landing during 1961-79 was 10,900 kg.

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[17] Seki, M. P., Fishery biologist, Southwest Fish. Cent. Honolulu Lab., Natl. Mar Fish. Serv., NOAA, Honolulu, HI 96822-2396, pers. commun. March 1983.

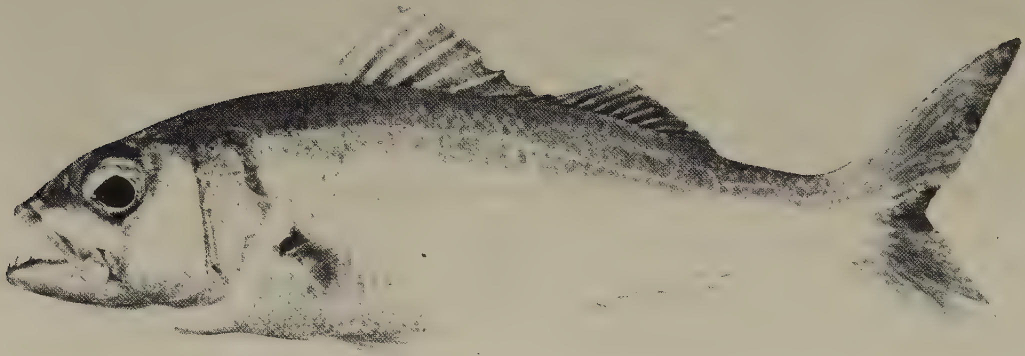

Figure 61.—*Etelis carbunculus*.

LUTJANIDAE — Gindai

by Alan R. Everson

Valid name	*Pristipomoides zonatus* (Cuvier and Valenciennes 1830) (Fig. 66)
Synonymy	*Tropidinius zonatus* Cuvier and Valenciennes 1830 *Serranus brighami* Seale 1901 *Apsilus brighami* Jordan and Evermann 1905 *Rooseveltia aloha* Jordan and Snyder 1907 *Rooseveltia brighami* Gosline and Brock 1960
Common and vernacular names	Brigham's snapper; ukiuki; kalikali; gindai; ukikikiki

Distribution

Caught incidentally with other bottom fishes at various islands and banks throughout the Hawaiian Archipelago. In the NWHI, caught from Necker Island to Pearl and Hermes Reef at depths between 102 and 238 m near ledges and drop-offs.

Distinguishing characteristics

D. X, 11; A. III, 8; P1. 16; LLps, 63-67; Gr. 7+13. Body short, stout, moderately compressed. Head large, bluntly conic, with a large slightly oblique mouth. Teeth on jaws, vomer, and palatines in villiform bands. Teeth in outer series on jaws enlarged, like canine. Single dorsal fin rather large, originating just over base of pectoral. Pectoral fairly long, about equal to head length, its tip reaching origin of anal fin (Masuda et al. 1975).

Distinguished from other snappers by its unique coloration. Four broad yellow bands on upper half of body, the last extending to the base of the caudal fin. Three light red bands about equal in width to the yellow bands between these yellow bands. Lower half of body yellow, head and snout bright golden red, underside of the body reddish (Jordan and Evermann 1905).

Life history

Little is known about the life history of gindai. Preliminary estimates of von Bertalanffy growth parameters were obtained using counts of annuli on otoliths. The von Bertalanffy growth equation for gindai is:

$$L_t = 43.1(1-e^{-1.09(t-1.51)})$$

where L_t = fork length (cm) expressed as a function of time t in years (Uchiyama and Tagami 1984). Estimates place a 3-year-old at 34.5 cm, 4-year-old at 40.2 cm, 5-year-old at 42.1 cm, and 6-year-old at 42.7 cm.

Gindai's reproductive cycle is probably similar to that of other snappers, and hydrated eggs develop in late summer; ovaries in ripe condition were collected in August at Laysan Island. The sex ratio is 57:43 (N = 106) in favor of females.

The functional length-weight relationship for 86 gindai ranging from 26.3 to 48.9 cm FL is:

$$W = 7.12 \times 10^{-9} L^{3.1878},$$

where W = weight (kg) and L = fork length (mm) (Uchiyama et al. 1984).

Gear and catch

Species is taken mainly by deep-sea handline. Gindai contributes little to the commercial bottom fish catch in the Hawaiian Islands. During 1961-70, the annual catch fluctuated between 212 and 1,680 kg and averaged 764 kg.

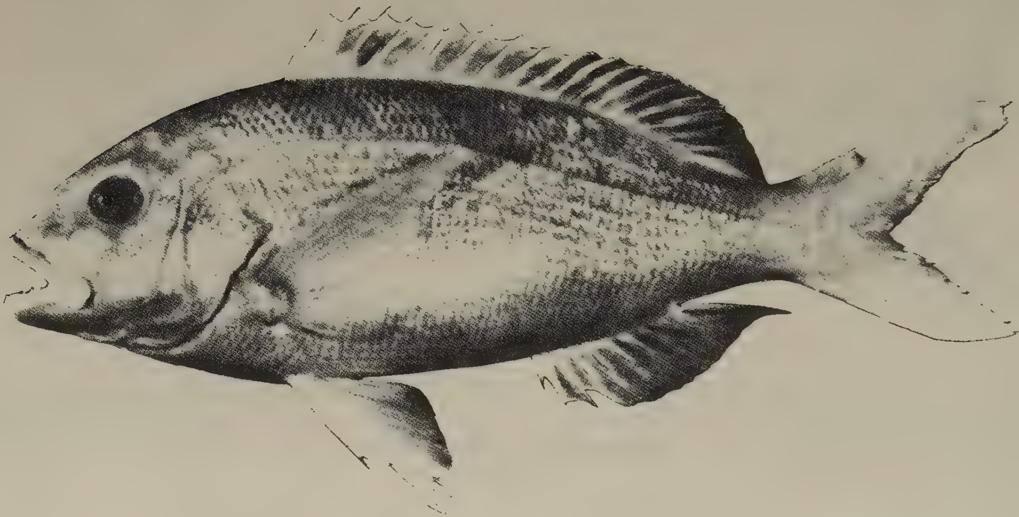

Figure 66.—*Pristipomoides zonatus*.

LUTJANIDAE

Kalekale

by Alan R. Everson

Valid name	*Pristipomoides sieboldii* (Bleeker 1857) (Fig. 65)
Synonymy	*Chaetopterus sieboldii* Bleeker 1857 *Chaetopterus dubius* Günther 1859 *Bowersia ulaula* Jordan and Evermann 1905 *Pristipomoides sieboldii* Jordan and Thompson 1911 *Ulaula sieboldii* Jordan and Jordan 1927 *Pristipomoides filamentosus* Fowler 1931 (from Kami 1973)
Common and vernacular names	Pink snapper; von Siebold's snapper; ulaula, koae, kalekale; kalikali

Distribution

Commonly taken around the main islands and banks. In the NWHI, taken on or near the bottom at depths between 91 and 219 m from Nihoa to Ladd Seamount.

Distinguishing characteristics

D. X, 11; A. III, 8; Gr. 21+5. Body long, slender, head bluntly conic, with rather short snout; moderate, somewhat oblique mouth; jaws about equal, with bands of villiform teeth on vomer, palatines, and tongue; eye rather large, its lower border in line with the axis of the body. Dorsal fin continuous without a notch; caudal fin densely scaled, widely forked, with equal lobes; pectoral fin slightly hooked (Jordan and Evermann 1905).

Kalekale is often confused with opakapaka. Distinguishing characteristics to separate species are: vomerines form an elongate diamond-shaped patch, with the blunt end of the diamond facing forward versus a triangular vomerine patch in opakapaka; kalekale generally smaller, eye larger, and more scales on the lateral line (Gosline and Brock 1960).

Kalekale silvery red with faint longitudinal blue lines in life. Dorsal and pectoral fins yellowish, ventral and anal fins clear, and tail fin reddish (Tinker 1978).

Life history

Life history information on kalekale is limited. It is an opportunistic bottom feeder and eats a variety of small fishes, crustaceans, larval squids, and tunicates (Kami 1973). The sex ratio is 78:22 (N = 162) in favor of females. The functional length-weight relationship for 128 kalekale ranging from 24.5 to 43.5 cm FL is:

$$W = 2.06 \times 10^{-9} L^{3.3702},$$

where W = weight (kg) and L = fork length (mm) (Uchiyama et al. 1984).

Gear and catch

Kalekale is taken mainly with deep-sea handline and occasionally by trap. Historically, kalekale has been a fairly important commercial species in Hawaii (Uchida et al. 1979). During 1961-63, annual catches rose slightly from about 8,300 to 11,000 kg, then declined steadily until 1970 when only 2,000 kg were landed. Since then, the catch has fluctuated within a narrow range from 2,600 to 4,400 kg. The average annual catch during 1961-79 was 4,700 kg.

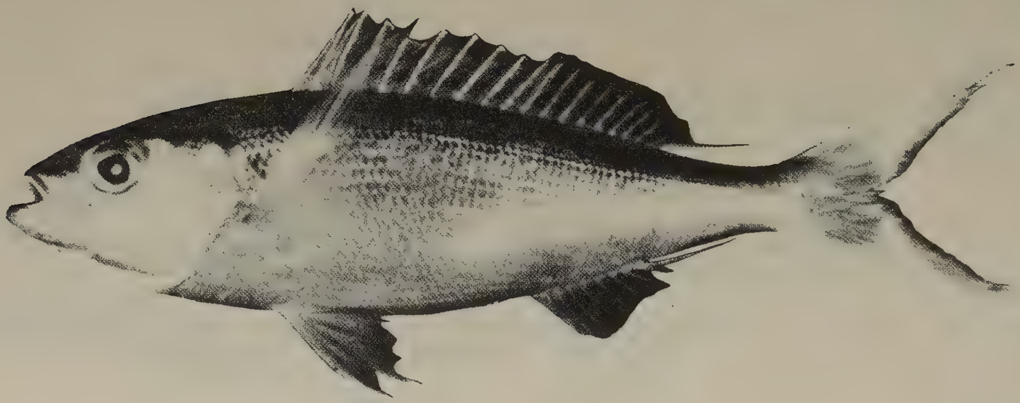

Figure 65.—*Pristipomoides sieboldii.*

8623

LUTJANIDAE — Onaga

by Alan R. Everson

Valid name	*Etelis coruscans* Valenciennes 1862 (Fig. 62)
Synonymy	*Etelis evurus* Jordan and Evermann 1905 *Etelis carbunculus* Gosline and Brock 1960
Common and vernacular names	Red snapper; ruby-colored snapper; longtail snapper; onaga; ulaula; ulaula koae

Distribution

Caught throughout the year around the main Hawaiian Islands and the NWHI from Bank 1 to Kure Atoll. Found slightly deeper (183 to 256 m) than the other Hawaiian snappers. It is caught on or near the bottom in areas of steep drop-offs, ledges, and pinnacles.

Distinguishing characteristics

D. X, 11; A. III, 8; Gr. 15+6 (Jordan and Evermann 1905). Body rather long, tapered, moderately compressed. Head longer than deep, bluntly pointed snout, large oblique mouth. Small bands of villiform teeth on the palatines and interior part of each jaw. Single row of small, wide set, slender canine teeth on the outer edge of each jaw, which also has a single canine tooth anteriorly. Deeply notched dorsal fin almost divided into two separate fins. Dorsal fin rays about equal in length. Anal fin similar in shape to soft dorsal. Caudal fin deeply notched producing long lobes; upper lobe longer; lobes get longer with age, taper into long caudal rays that are characteristic of onaga.

Color brilliant rose red.

Life history

Little is known about the life history of onaga in the NWHI. Their reproductive cycle is probably similar to that of ehu. Ripe and near ripe ovaries were collected in August and September at Raita Bank. However, onaga ovaries were collected only during summer months.

A linear growth stanza derived from five age determinations provided the following length-age estimates: 21.0 cm FL at 1 year and 58.1 cm at 2 years (Uchiyama and Tagami 1984).

The functional length-weight relationship for onaga 48.0 to 88.0 cm FL is:

$$W = 2.99 \times 10^{-8} L^{2.9003},$$

where W = weight (kg) and L = fork length (mm) (Uchiyama et al. 1984).

The sex ratio of fish caught in the NWHI is 69:31 (N = 64) in favor of females. The mean weight of males is 4.28 kg and for females 5.45 kg in the NWHI.

Gear and catch

The species is caught by deep-sea handline. Historically, onaga has been an important commercial species in Hawaiian waters (Uchida et al. 1979). It is a valuable fish commanding high wholesale prices (see footnote 14). During 1961-68, annual catch increased from 19,500 to 31,700 kg, but from 1969 to 1974, the annual catch decreased and fluctuated between a narrow range of 17,300 and 22,800 kg. The annual catch rose sharply to 30,000 kg in 1975 and 41,100 kg in 1976 then declined steadily to 22,100 kg in 1979. The average annual catch from 1961 to 1979 was 25,900 kg.

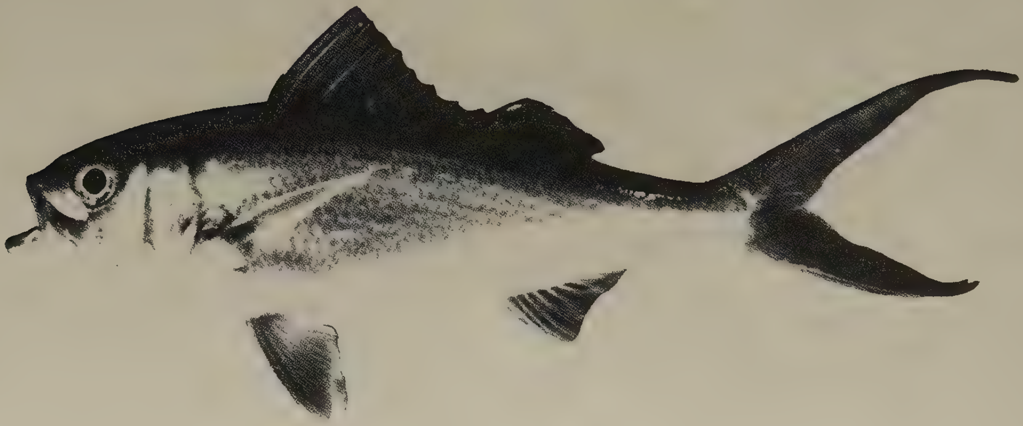

Figure 62.—*Etelis coruscans.*

8624

OFFSHORE ENTRAINMENT OF ANCHOVY SPAWNING HABITAT, EGGS, AND LARVAE BY A DISPLACED EDDY IN 1985

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ABSTRACT

In early 1985, a recurrent anticyclonic eddy, normally located about 400 km southwest of Point Conception, was displaced toward the offshore limit of the northern anchovy spawning range in the Southern California Bight. The anomalous location of the eddy, and surface flow patterns associated with it were determined from hydrographic data and satellite imagery. Productive surface waters of 14°-15°C, characteristic of the preferred spawning habitat of northern anchovy, were entrained from within the Southern California Bight by the eddy. Eggs were found 150 km farther offshore than in 1980-84, because of a combination of spawning habitat extension and advection. The eggs and subsequent larvae were removed from the usual larval feeding grounds within the bight. This extraordinary displacement apparently had little or no effect on recruitment in fall 1985.

RESUMEN

A principios de 1985, un vórtice anticiclónico de carácter periódico, normalmente ubicado alrededor de 400 km al Sureste de Point Conception, fue desplazado hacia el límite externo de la zona de desove de la anchoveta norteña en la Bahía del Sur de California. La ubicación anómala de este vórtice, y los patrones de circulación superficial asociados con el mismo fueron determinados por medio de información hidrográfica e imágenes de satélite. Aguas superficiales productivas con temperaturas de 14°-15°C, características del habitat de desove preferido de la anchoveta norteña, fueron atrapadas por el vórtice desde el interior de la Bahía del Sur de California. Se encontraron huevos a 150 km, mar adentro, en relación a aquellos colectados en 1980-84, debido a una extensión del habitat combinada con una advección de los productos de desove. Estos huevos y las posteriores larvas fueron sacados de las áreas de alimentación larval normales en la bahía. Este desplazamiento extraordinario de los productos de desove tuvo, aparentemente, muy poco o ningún efecto sobre el reclutamiento en el otoño de 1985.

INTRODUCTION

The Southern California Bight is the center of spawning activity for many pelagic fishes, including the large central stock of northern anchovy (*Engraulis mordax*). The bight is a particularly favorable spawning habitat, with a semienclosed gyral pattern of geostrophic flow (the Southern California Eddy) over a wide and topographically complex continental shelf; a relatively stable density structure of near-surface waters; and weak offshore Ekman transport and turbulent mixing (Husby and Nelson 1982; Parrish et al. 1983). The main axis of the California Current and the persistent eddy field seaward of that axis are normally farther from the coast along southern California than they are to the north of Point Conception (Figure 1). Peak anchovy spawning in February-April coincides with the seasonal minimum of offshore velocity in the surface mixed layer (Bakun 1985). Thus, minimizing the offshore dispersion of eggs and larvae from the coastal spawning habitat appears to be an important component of the spawning strategy of northern anchovy and other fishes in the Southern California Bight (Parrish et al. 1981).

This generalization is based on mean patterns of spawning activity and environmental variables. The Southern California Bight, however, is part of the highly variable California Current system, which is dominated by low-frequency, interannual changes in physical and biological factors (Chelton et al. 1982). Much of this variability is caused by tropical El Niño and mid-latitude warm events (Norton et al. 1985), which have had demonstrated effects on northern anchovy spawning activity (Fiedler et al. 1986).

The anchovy is a multiple spawner, with each female producing several batches of eggs per year. Eggs remain near the surface and hatch two to four days after spawning. Some spawning activity is observed year-round, but three-quarters of the yearly spawnings occur in February-April (Parrish et al., in press). Abundance and spatial distribution of anchovy eggs have been measured on biomass surveys during peak spawning months since 1980 (Figure 2. Stauffer and Picquelle 1980, 1981[1]; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986).

Substantial variations in egg distribution were caused by the 1982-84 California El Niño. In 1983 the

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[Manuscript received February 12, 1986.]

[1] Stauffer, G.D., and S.J. Picquelle. 1981. The 1981 egg production estimates of anchovy spawning biomass. Southwest Fisheries Center, unpublished report

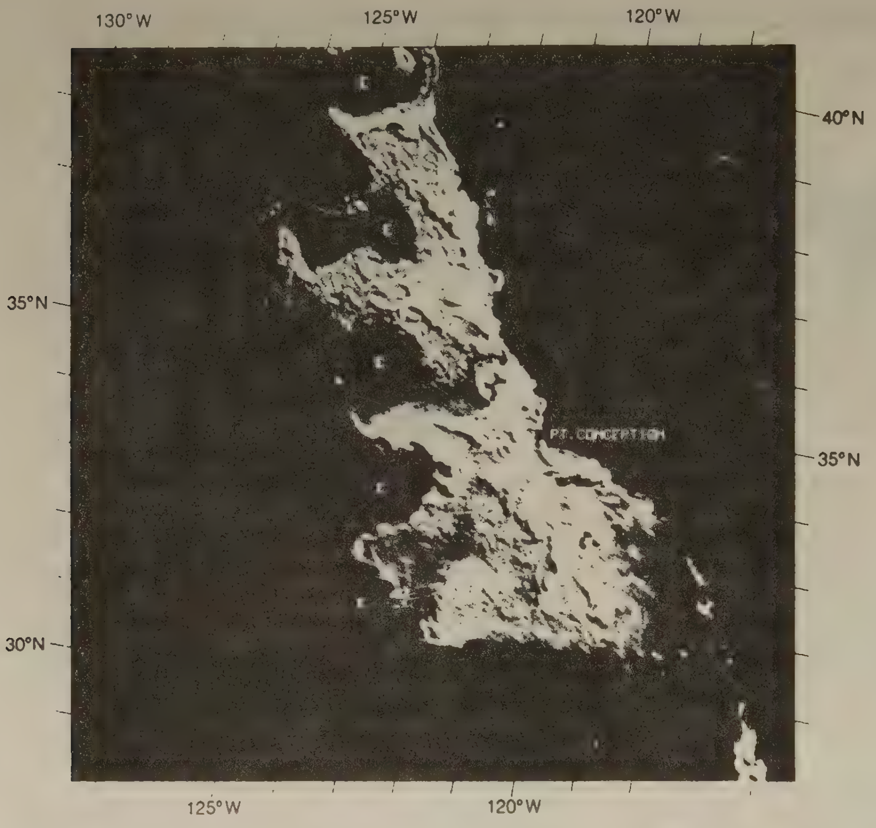

Figure 1. CZCS phytoplankton pigment image, June 15, 1981, showing a series of offshore eddies (E) in the California Current region off California. The recurrent eddy is the second from the bottom, to the left of Point Conception. Distance of eddies from coast increases north to south, from 100 to 400 km. Lighter shades indicate higher pigment concentrations on a logarithmic scale, with an additional enhancement to emphasize gradients.

boundary normally formed by the ~14°C surface isotherm had shifted far to the north of Point Conception; spawning range extended unusually far to the north, as well as offshore in the region of the Channel Islands. In 1984 the cold-water boundary was present, but spawning range again extended somewhat farther offshore than in 1980-82. On the 1980-84 surveys, eggs were sampled as far as 250 to 280 km from shore in the central region of the Southern California Bight (i.e., between CalCOFI lines 86.7 and 92).

The 1985 egg distribution was very unusual. First, small but significant numbers of eggs were found in cold (< 13°C) water to the north of Point Conception. Then, large numbers of eggs began to be taken along line 90. Sampling was extended offshore to station 80 on lines 91.7 to 95. Eggs were found up to 400 km offshore on these lines, 120-150 km beyond the farthest offshore eggs in 1980-84.

The anomalous offshore extension of the 1985 egg distribution would have important consequences for the stock if these eggs, and the larvae hatched from them, were irretrievably lost from inshore larval feeding grounds. What could have caused the peculiar egg distribution pattern? Offshore Ekman transport (coastal upwelling) is a primary mechanism of offshore transport in eastern boundary current systems. However, coastal upwelling off California is near its seasonal minimum in February and does not produce extensive coastal jets or plumes within the Southern California Bight. Another mechanism is needed to explain the observations.

An anticyclonic eddy located about 400 km SW of Point Conception is a recurrent component of the offshore eddy field of the California Current system; January-April 1949-65 CalCOFI data indicate that its mean postion is 32.1°N, 123.4°W, ± 1.2° (Simpson et al. in press). A sporadic, but not unusual, phenomenon associated with this eddy has been noted: onshore displacement may cause enhanced entrainment of cool coastal water and its associated biological community (Haury et al. in press). In this paper, I will exploit the extensive, detailed, and repetitive coverage of the sea surface by satellite-borne sensors to locate the eddy and estimate surface flow associated with it. I wish to

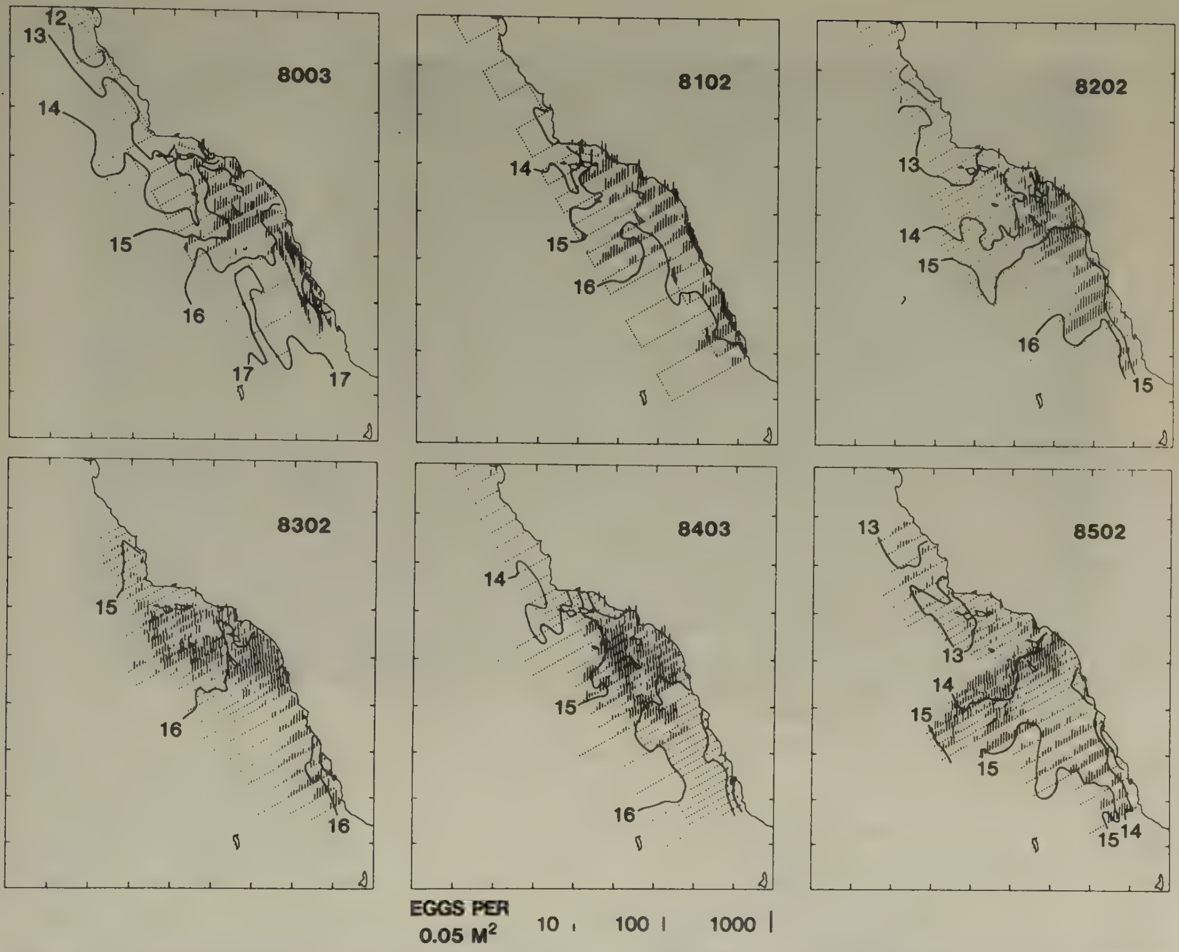

Figure 2. Surface isotherms (°C) and anchovy egg distributions on anchovy biomass cruises (CalCOFI 8003-4, 8102, 8202, 8302, 8403, and 8502). From Fiedler et al. (1986).

thank Jim Simpson for pointing out the possible manifestation of the displaced eddy in the data from CalCOFI cruise 8502.

METHODS

Satellite data were received, archived, and processed at the Scripps Satellite Oceanography Facility. Thermal infrared data from channel 4 (11 μm) of the Advanced Very High Resolution Radiometer (AHVRR) on the NOAA-7 and NOAA-9 satellites were corrected for the effect of thin low clouds, when necessary, using channel 2 (0.7-1.1 μm) near-infrared data (Gower 1985). No further correction was implemented for absorption of sea-surface radiance by atmospheric water vapor. Although multichannel correction algorithms produce more accurate temperature estimates, they do so at the cost of amplifying the noise in the sensor signal. Preserving small-scale patterns of sea-surface temperature variability was considered a higher priority for this study.

Visible radiance data from the Coastal Zone Color Scanner (CZCS, Nimbus-7 satellite) were processed using an algorithm based on Gordon et al. (1983) to remove effects of Rayleigh and aerosol scattering and to derive phytoplankton pigment concentrations from corrected blue/green radiance ratios. Surface flow patterns were derived by tracking movement of submesoscale features in sequential AVHRR images (Vastano and Borders 1984).

RESULTS

In Figure 3, two AVHRR sea-surface temperature images show mesoscale variability off southern California in January 1984 and 1985. In both images, the

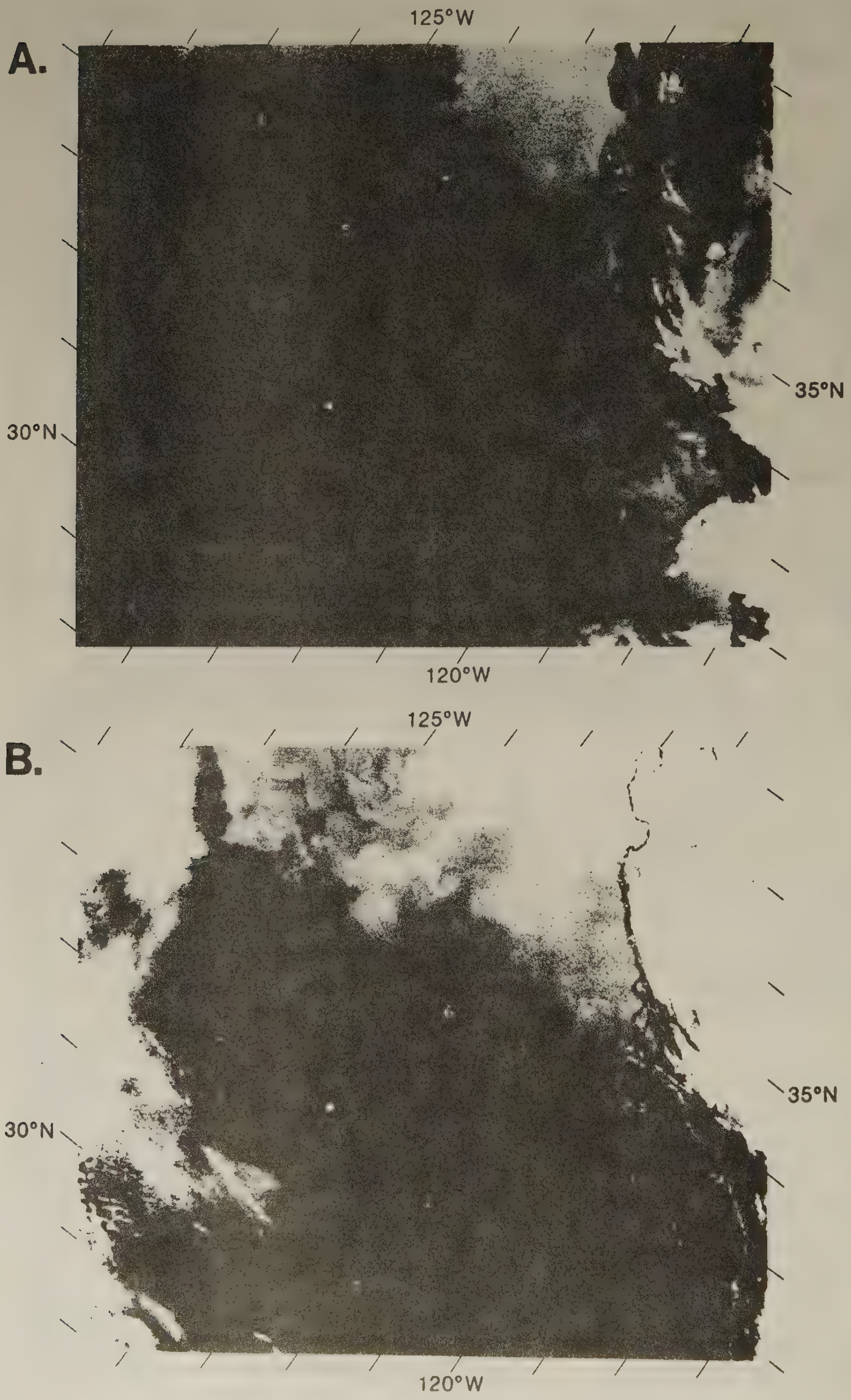

Figure 3. AVHRR sea-surface temperature images from *(A)* January 26, 1984 (1 = anticyclonic eddy, 2 = cold streamer, 3 = warm streamer, 4 = cold streamer from coast, 5 = secondary warm streamer) and *(B)* January 1, 1985 (6 = anticyclonic eddy, 7 = cold streamer from coast, 8 = cold-water plume from Point Conception). The asterisk (*) marks the mean January-April location of the recurrent eddy (Simpson et al., in press). Water temperatures range from 10.5°C (light grey) to 17°C (dark grey).

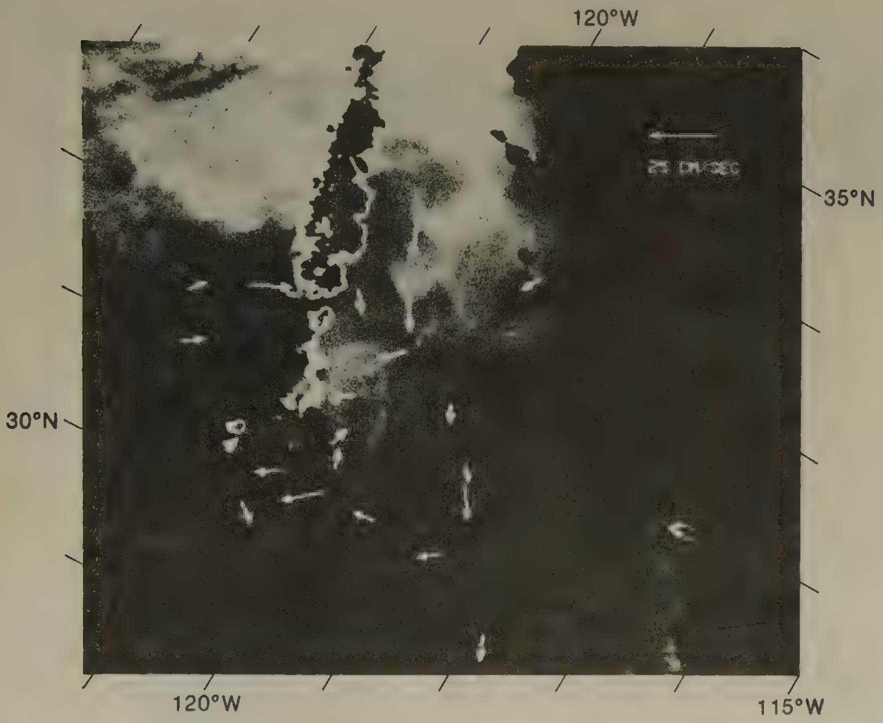

Figure 4. AVHRR sea-surface temperature image from February 21, 1985, with surface current vectors (arrows) derived from movements of submesoscale features visible on February 21 and 24, 1985. Temperatures range between 10° and 13.6°C. Clouds and land are masked with black.

coldest water (lighter grey shades) is along the coast to the north of Point Conception. This is California Current water augmented by seasonally weak coastal upwelling. The cold surface water extends south of Point Conception as a streamer or plume that separates from the coast. This pattern is obscured by clouds in Figure 3a, but is clearly visible in Figure 3b, where warmer nearshore water in the Southern California Bight can also be seen. The warmest water in both images is found to the south and offshore.

On January 26, 1984, a warm-water anticyclonic eddy is clearly visible at 34.2°N, 126.4°W (Figure 3a). This is 360 km northwest of the mean historical position, at the extreme of the range observed by Simpson et al. (in press). A well-defined cold streamer, with a source outside the image to the north, is wrapped around the inshore side of the eddy. A warm streamer from an offshore, oceanic source is wrapped around the offshore side of the eddy. The temperature of surface water within the eddy is intermediate between the temperatures of the surrounding warm and cold streamers. A large cold streamer (~400 km long) extends from the coast north of Point Conception out toward the eddy. Instead of becoming entrained by the eddy, this streamer is deflected to the south around a secondary warm streamer surrounding the inshore edge of the eddy.

On January 1, 1985, a warm-water anticyclonic eddy is at 33.8°N, 122.5°W—370 km east of the January 1984 eddy and 210 km northeast of the mean position (Figure 3b). A cold streamer flowing along the southern edge of the eddy is anchored on the coast in the vicinity of Point Conception and can be traced almost 500 km offshore. Some water from within the Southern California Bight appears to be entrained in this streamer.

On February 21, 1985, the eddy was located at 32.6°N, 122.5°W (Figure 4). It was then 130 km south of its position on January 1 and 100 km east-northeast of the mean postion. A surface velocity field derived from the February 21 and 24 images is included in Figure 4. Current vectors were more easily measured at the edges of the eddy than in the cool coastal water mass inshore of the eddy, because the submesoscale features serving as tracers are most visible at strong temperature gradients. Although cloud cover prevented complete coverage of the eddy, and the discernable flow pattern is complex, anticyclonic rotation is apparent on the northern and inshore edges, where velocities are 7-15 cm/sec, dominated by an offshore component of 7-10 cm/sec.

Figure 5 is a Coastal Zone Color Scanner image showing that the cool coastal water being entrained offshore by the eddy was relatively rich in phytoplank-

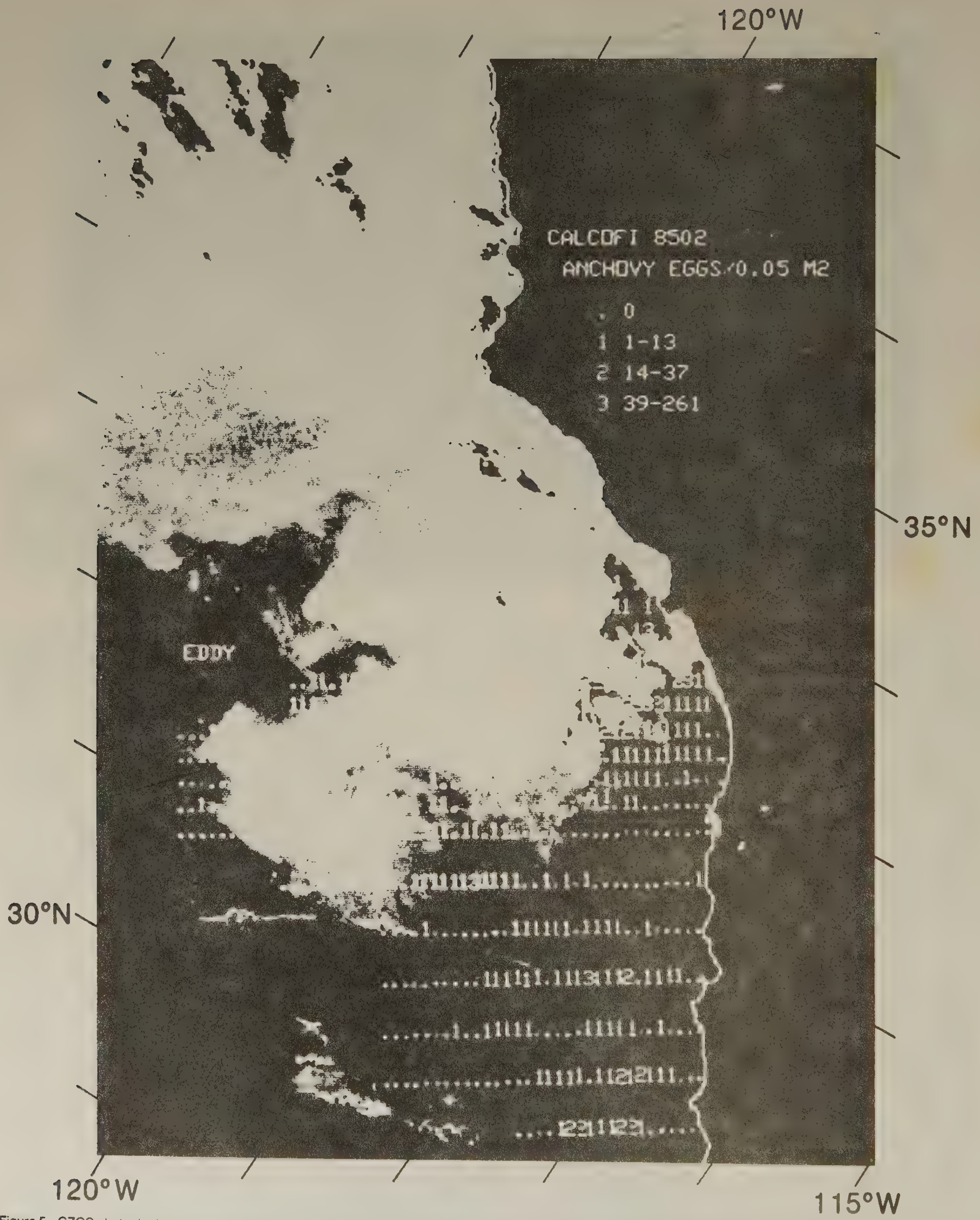
120°W
CALCOFI 8502
ANCHOVY EGGS/0.05 M2
. 0
1 1-13
2 14-37
3 39-261
35°N
EDDY
30°N
120°W
115°W

Figure 5. CZCS phytoplankton pigment image from February 28, 1985. Pigment concentrations range between 0.12 and 4.7 mg m^3 (dark to light). Clouds and land are masked with black. Relative abundance of anchovy eggs in vertical egg tows (CALVET) on CalCOFI cruise 8502, R/V *David Starr Jordan*, January 28-March 8, 1985.

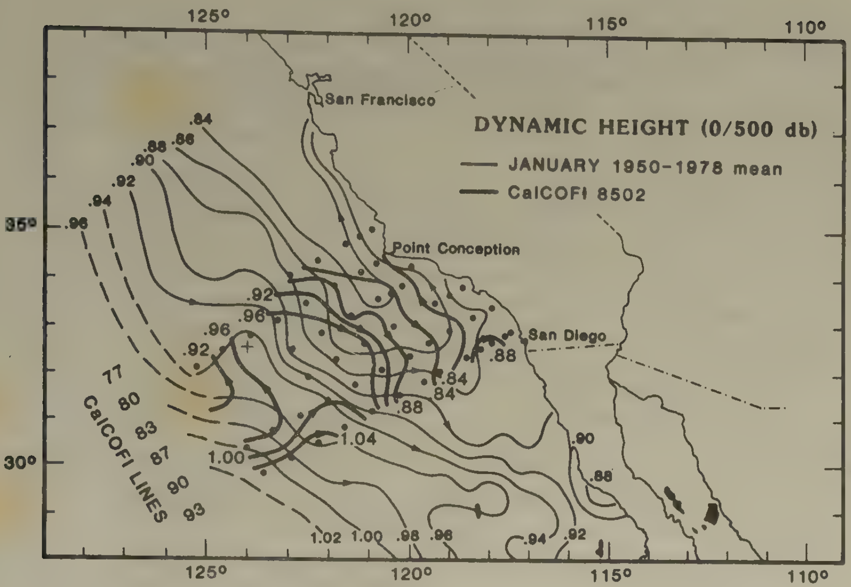

Figure 6. Dynamic height and geostrophic flow at the surface: January 1950-78 mean (Lynn et al. 1982) and CalCOFI cruise 8502, February 19-March 5, 1985 (Scripps Institution of Oceanography 1985). + = mean postion of recurrent anticyclonic eddy (Simpson et al., in press).

ton pigment. The offshore extension of anchovy eggs is contained in this cool, rich surface water. Note, however, that there are few eggs in the even colder and richer water to the north toward Point Conception.

DISCUSSION

In the mean January hydrography, this recurrent anticyclonic eddy appears as a local elevation in dynamic height within a geostrophic current meander (Figure 6), and as local depressions of isopycnal surfaces (sigma-t = 25.0 in the top of the thermocline at ~80 m; sigma-t = 25.8 at ~140 m; and sigma-t = 26.6 at ~280 m; Lynn et al. 1982). Dynamic topography at the sea surface in February 1985 shows an unusual pattern of meanders centered at 32°N, 122°W (Figure 6). The local high, and the direction of flow on three sides of it suggest that the eddy was embedded within this pattern. The revised CalCOFI grid, with no offshore sampling between lines 80 and 90, unfortunately missed the center of this eddy. However, the data show the enhanced entrainment of coastal water expected from such a displacement: the direction of surface flow at coastal stations along CalCOFI lines 90 and 93, inshore of the eddy, was more offshore than the long-term mean. The observed egg distribution is consistent with entrainment in anomalously strong offshore flow associated with the displaced eddy: the offshore extension of anchovy eggs is within the region of anomalous offshore flow.

Power (in press) analyzed larval anchovy drift from the spawning center in the Southern California Bight. His 30-day simulation model of advection-diffusion incorporated mean seasonal geostrophic currents and Ekman transport and a constant eddy diffusivity. In March, most larvae move inshore from the points where they were spawned. Monthly mean offshore Ekman velocities in the bight range between .05 and 2.0 cm/sec, assuming negligible Ekman transport below 50 m (Husby and Nelson 1982). Power found that significant seaward transport of larvae occurred only if Ekman velocities were increased to three times the long-term mean, or up to 6 cm/sec.

During an intensive study in January 1981, the anticyclonic eddy was located at 32.4°N, 124°W and was found to be entraining both cold coastal waters and warm oceanic waters into its surface and near-surface layers. In this "normal" case, the source of the coastal waters was north of Point Conception (Simpson et al. 1984). Satellite imagery shows that this eddy was displaced 100-200 km inshore of the normal position in January and February 1985. Surface waters from within the Southern California Bight were entrained toward the eddy. Apparent offshore velocities were up to 10 cm/sec, or five times greater than normal mean offshore Ekman velocities.

Eggs that hatch in three days could move only 30 km at this speed. Therefore, anomalous advection of eggs cannot entirely explain the 150 km offshore extension. Spawning must have been taking place offshore of the normal range. Ken Mais provides maps of major concentrations of adult anchovies in the central stock from February acoustic and midwater trawl surveys of the central stock (California Department of Fish and Game Cruise Reports 80-A-1, 81-X-1, 82-X-1, 83-X-1, 84-

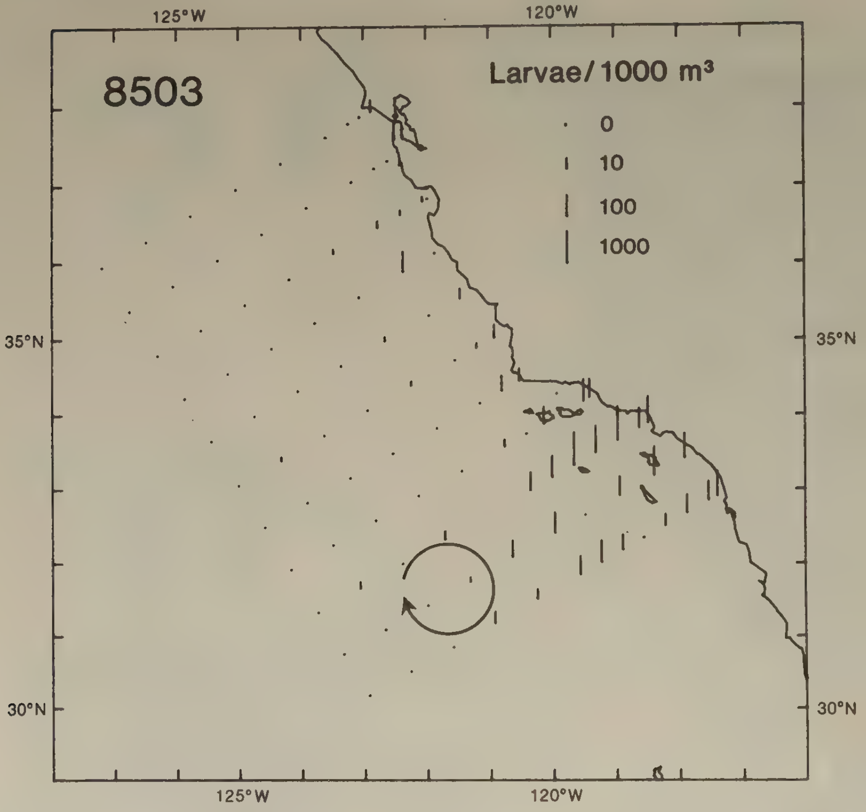

Figure 7. Anchovy larvae abundance from bongo net tows, 333-μm mesh, on CalCOFI cruise 8503, R/V *McArthur*, March 15–April 5, 1985. The location of the eddy on February 21, 1985, is indicated schematically.

X-1, and 85-X-1). These maps show a maximum offshore extent of anchovies of 230 km in 1985, compared with 80-190 km (mean = 142 km) in 1980-84. Mais reported that the 1985 distribution was more offshore and southward than in any previous survey, and that "the bulk of the population was located in an arc of 80 miles west to south, and 30 miles east to south of San Clemente Island." This distribution encompasses the region of anomalous offshore flow illustrated in Figure 6.

Adult spawners in winter 1985 moved offshore within the cool coastal water mass being entrained by the displaced eddy. The eggs spawned by these fish were advected for a short distance by this offshore flow. We can assume that offshore advection continued as the eggs hatched and larvae developed. Ultimately, the larvae may have been trapped in the surface convergence within the eddy or spun off to the south and offshore. A few larvae were found offshore in the vicinity of the eddy in March 1985 (out to station 100 on line 87; Figure 7). Unfortunately, no sampling was done south of the U.S.-Mexico border.

Available evidence indicates that the displacement of spawning habitat and products had little, if any, effect on recruitment of the 1985 anchovy year class. Central stock spawning biomass in February 1985 was about average for the post-1979 period (Bindman 1986). A September California Department of Fish and Game anchovy recruitment survey north of the U.S.-Mexico border found evidence of a relatively weak 1985 year class: mean catch rate of juveniles ranked seventh among nine surveys conducted since 1976 (K. F. Mais, California Department of Fish and Game Cruise Report 85-X-14). A limited trawl survey in February-March 1986 again found a relatively small proportion of 1985 year-class fish (K. F. Mais, California Department of Fish and Game Cruise Report 86-X-4). However, the year class appeared relatively strong in the Ensenada fishery south of the border in fall 1985 (R. Methot, Southwest Fisheries Center, pers. comm.).

The best estimate as of April 1986 is that the 1985 year class is neither stronger nor weaker than expected from the 1985 spawning stock. Two major environmental perturbations in recent years—the 1982-84 California El Niño and the displaced offshore eddy in 1985—have caused observable changes in central stock spawning activity without a resultant effect on stock size. The northern anchovy seems to be resistant to such perturbations, perhaps because of compensatory responses in the juvenile stage that we are only beginning to sample adequately.

ACKNOWLEDGMENTS

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Effects of California El Niño 1982–1984 on the northern anchovy

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ABSTRACT

El Niño caused physical and biological changes in the northern anchovy habitat off southern California. Anomalous sea surface temperatures, surface currents, mixed layer depths, and plankton biomass levels began to appear in late 1982 and persisted into 1984. Growth of juvenile and adult anchovy slowed during El Niño, probably due to reduced availability of zooplankton prey. A decrease in size-at-age in early 1983, with a recovery in late 1984, can be explained by movements of the stock and the latitudinal cline in size-at-age. Spawning range expanded in 1983 due to shifts in sea surface temperature boundaries. Early larval mortality was unusually high in the yolk-sac stage. Fecundity per unit spawning biomass was low in 1983, due primarily to a high proportion of first-year spawners. Size-at-age was very low by spring 1984, but specific fecundity was surprisingly high. Although El Niño had a variety of significant effects on the northern anchovy, the stock seems to have recovered in 1985.

1. Introduction

The northern anchovy, *Engraulis mordax,* in the California Current and the anchoveta, *Engraulis ringens,* in the Peru Current, are ecological analogs: relatively small, short-lived, pelagic planktivores living in highly variable eastern boundary current systems (Parrish *et al.,* 1983). Sardine and anchovy stocks are notoriously variable and prone to collapse under fishing pressure exacerbated by environmental stress. Notable examples in the eastern Pacific have been the California sardine in the late 1940's (Murphy, 1966) and the Peruvian anchoveta in the early 1970's (Walsh *et al.,* 1980).

Three distinct subpopulations or stocks of northern anchovy have been differentiated along the west coast of North America (Vrooman *et al.,* 1981; see Fig. 1). The large central stock spawns in the Southern California Bight between Point Conception (34.5N) and Punta Baja (30N). Since 1980, spawning biomass of the central stock has been estimated by the egg production method (Parker, 1980) at the La Jolla

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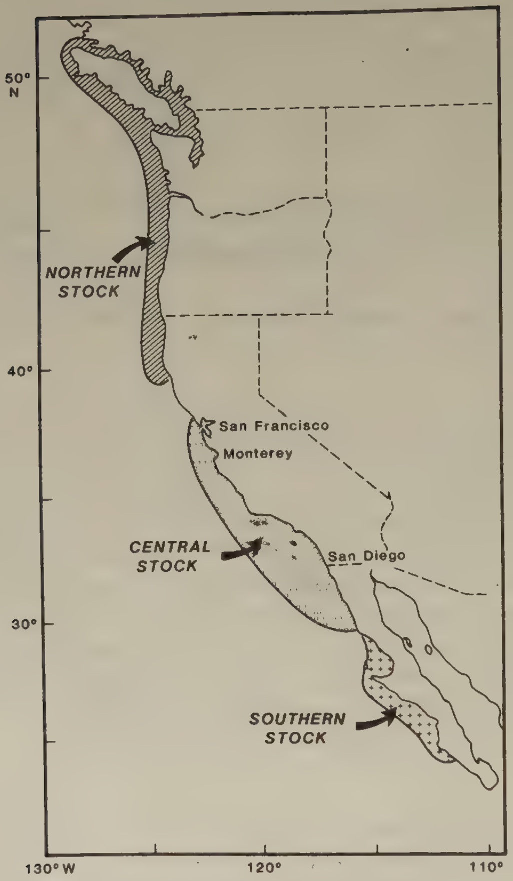

Figure 1. Northern anchovy stocks.

Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service (NMFS).

The egg production method defines spawning biomass as the daily production of eggs divided by the daily specific fecundity of the adult population. Daily egg production is derived from an ichthyoplankton survey and egg development rates measured in the laboratory. Daily specific fecundity is derived from a trawl sample yielding estimates of average female weight, batch fecundity, sex ratio, and the proportion of females spawning each night. Trawls and egg tows are taken concurrently on a survey conducted during the seasonal peak of spawning activity, from February to April. Some spawning activity is observed year-round, but 73% of all spawnings occur in February to April (Parrish *et al.*, 1986). Larval growth and mortality can also be estimated from the ichthyoplankton samples. Juveniles and adults are sampled and aged two or three times a year by the California Department of

Table 1. Northern anchovy central stock population parameter estimates, 1980–1985. Spawning biomass and spawning female weight from Bindman (1985). Year class size from Methot (in prep.), 1985 value is a preliminary estimate subject to change.

	1980	1981	1982	1983	1984	1985
Spawning biomass, 10^3 metric tons (c.v.)	870 (.262)	635 (.216)	415 (.257)	652 (.211)	306 (.165)	458 (.188)
Spawning female weight, g	17.5	13.4	18.8	11.2	12.0	14.5
Mean age in February, yrs	1.80	1.80	2.46	1.29	1.76	1.46
Year class size, 10^9 fish	63	14	45	35	109	(39)

Fish and Game (DFG) Sea Survey program. Table 1 lists some results of NMFS and DFG surveys in 1980–1985.

Spawning biomass of the central stock has been declining since 1975 (Fig. 2). The 1984 biomass was the lowest since 1962, but the 1985 estimate may indicate a recovery. Catch increased until 1981, largely from intense Mexican fishing effort, but never reached a level sufficient to explain the decline in spawning biomass. The stock was dominated by 2 to 4-year-old fish until 1979, but 1 and 2-year-olds have dominated since the recruitment of a very large 1978 year class (Mais, 1981). A relatively large 1982 year class was recruited in 1983: the 1982 year class made up 75% of the stock in February 1983. Such a small and young stock is particularly vulnerable to environmental stresses because it may be unable to recover from successive year-class failures. Fecundity of the northern anchovy is strongly age-dependent (Parrish *et al.*, 1986).

An unusually strong and well-documented El Niño caused substantial changes in the eastern equatorial Pacific from mid-1982 to August 1983. Changes in the

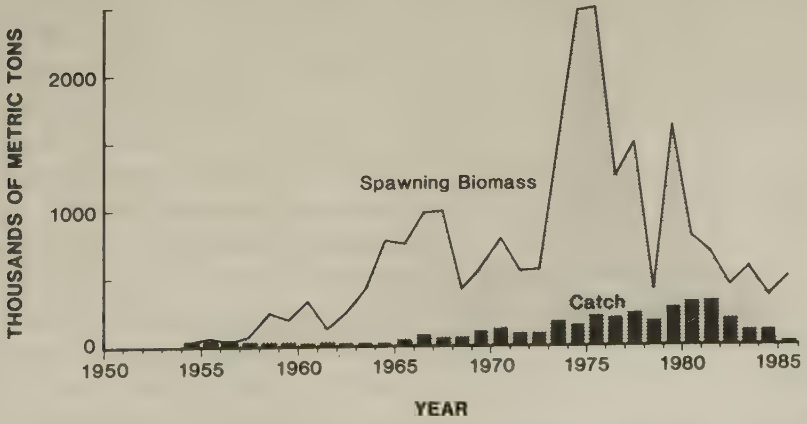

Figure 2. Spawning biomass of northern anchovy central stock and total U.S. and Mexican catch (MacCall and Methot, 1983).

California Current system were observed beginning in late 1982 (McGowan, 1983; Simpson, 1983; Fiedler, 1984a). Fiedler (1984b) provided a preliminary report of effects of the California El Niño on the northern anchovy central stock, based on data available by the end of 1983. This report is a more complete review of effects manifested in data from NMFS biomass surveys and DFG Sea Surveys and in the derived stock and spawning parameters estimated for management purposes. We compare the El Niño years of 1983 and 1984 with the 1980–1985 "anti-El Niño" years (1980–1982 and 1985). Much of the data reported here have appeared previously in internal reports, but we present original analyses and synthesis.

2. Methods

a. Environmental time series. Water temperature and sea level have been recorded since about 1920 at Scripps Pier in La Jolla, California (32.9N, 117.3W). The center of the central stock spawning range in 1980–1984 was ~60 km directly offshore of this coastal station. Monthly surface temperature anomalies were obtained from Smith (1985a). Monthly mean sea levels (J. Simpson, Scripps Institution of Oceanography, pers. comm.) were corrected for a secular rise of +0.21 cm/yr, but not for inverse barometric effects, before calculating monthly anomalies. Both series were then smoothed with a resistant nonparametric algorithm (Ryan *et al.,* 1981) to remove high-frequency spikes and isolate interannual variability.

We compared monthly Scripps Pier surface temperature anomalies to monthly sea surface temperature anomalies based on ship, buoy and satellite observations and published in the Oceanographic Monthly Summary (NOAA/National Weather Service). By simple linear regression over 48 months from 1981 through 1984, Scripps Pier temperature anomalies explain 59.1% of the variability of sea surface temperature anomalies in an area covering the center of the northern anchovy habitat in the Southern California Bight (31–34N within 150 km of the coast). Therefore, sea surface temperature variability in the anchovy habitat is adequately described by the Scripps Pier surface temperature record.

b. Egg production. Spawning biomass surveys for egg production estimates since 1980 have covered coastal waters to ~250 km offshore between San Francisco, California and Punta Baja, Baja California (Table 2). Planktonic eggs and small larvae were sampled at 7.5 km intervals with a 25 cm net (333 μm mesh in 1980–1982 and 150 μm mesh since 1983), towed vertically to the surface from a depth of 70 m in one minute (CALVET). Ichthyoplankton samples were collected with a 71 cm Bongo net of 505 μm mesh, towed obliquely from a depth of 200 m (CALBOBL). This net effectively samples anchovy larvae <10 mm with measured corrections for size-dependent extrusion and avoidance during daylight (Lo, 1983). Adults were sampled with a 15 m midwater trawl with a 6 mm mesh liner in the cod end.

The egg production estimate of spawning biomass is equal to daily production of

Table 2. CalCOFI anchovy biomass surveys for egg production estimates.

Cruise	Dates	# CALVET Tows
8003	20 Mar–10 Apr 1980	537
8004	12 Apr–29 Apr 1980	424
8102	12 Feb–10 Mar 1981	690
8104	31 Mar–27 Apr 1981	444
8202	18 Jan–9 Mar 1982	993
8302	4 Feb–1 Apr 1983	850
8403	7 Feb–30 Mar 1984	944
8502	28 Jan–8 Mar 1985	909

eggs divided by specific fecundity. Daily egg production is estimated by extrapolating staged egg abundances back to the time of spawning, using temperature-dependent egg development rates measured in the laboratory. Specific fecundity, the daily production of eggs per unit biomass, is calculated as follows:

$$\text{Specific fecundity} = \frac{R\,S\,F}{W}$$

where

R = female fraction by weight,

S = spawning incidence, day^{-1},

F = batch fecundity, eggs,

W = spawning female weight, g.

R, S, F, and W are estimated from subsamples of the midwater trawl catches. Details and assumptions of the egg production method are covered in Lasker (1984).

c. *Larval mortality*. Survival curves for yolk-sac larvae (up to 4.0 mm) and first-feeding larvae (4.0–6.0 mm) were generated from CALVET staged larval counts. Shrinkage corrections were based on Theilacker (1980). Extrusion of larvae ≤4.0 mm through the 333 μm mesh used through 1982 was corrected according to Lo (1983). Avoidance of the CALVET net during daylight by 3.75–6.25 mm larvae was measured as night/day catch ratios in 0.5 mm size intervals and corrected by the following factors: 1.17, 1.34, 1.99, 2.52, and 2.92. Ages and durations of 0.5-mm stages were calculated from Gompertz growth equations for yolk-sac (Lo, 1983) and feeding larvae (Lo, NMFS/Southwest Fisheries Center, pers. comm.). Growth is temperature-dependent for yolk-sac larvae; growth of feeding larvae shows little temperature-dependence within seasons (Methot, 1981). Production of hatching eggs was calculated from estimates of production of spawned eggs and egg mortality from analyses of CALVET egg counts.

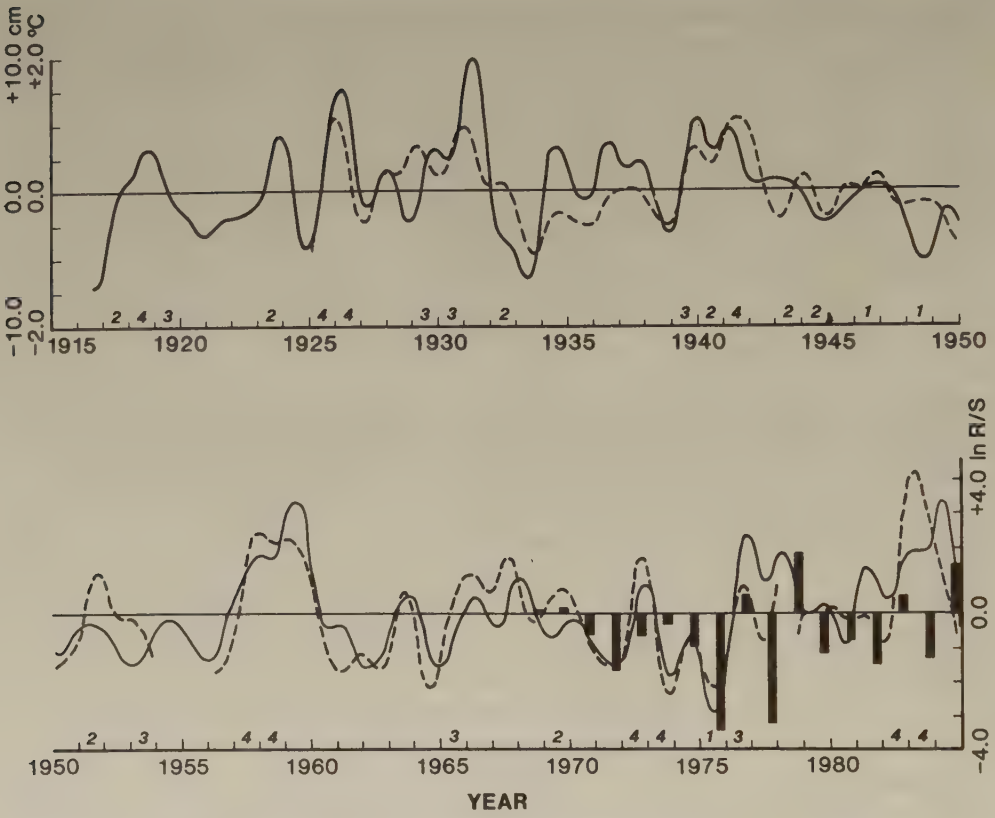

Figure 3. Smoothed monthly anomalies of surface temperature (°C, solid line) and sea level (cm, dashed line) at Scripps Institution of Oceanography Pier in La Jolla, California (32.9N, 117.3W). Numbers are rankings of ENSO events (Rasmusson, 1984): 1 = weak, 2 = moderate, 3 = strong, 4 = very strong (ln R/S = recruitment index, see text).

d. Age-length. The California Department of Fish and Game regularly conducts an anchovy central stock biomass survey in February–March and a recruitment survey in September–October. Recruitment surveys are confined to nearshore waters within the 100 m isobath. Nighttime 15 m midwater trawl samples are taken to determine age and size composition. These data were kindly provided by Ken Mais, California Department of Fish and Game. Von Bertalanffy growth curves were fit to the mean sizes at age for each of the 1978 to 1984 year classes. By this model, growth rate decreases linearly with size and seasonal variations are ignored.

3. Results

a. Historical relationship to El Niño. Interannual variability of surface temperature and sea level in the Southern California Bight is dominated by large positive anomalies every few years, usually corresponding to ocean-wide El Niño/Southern Oscillation

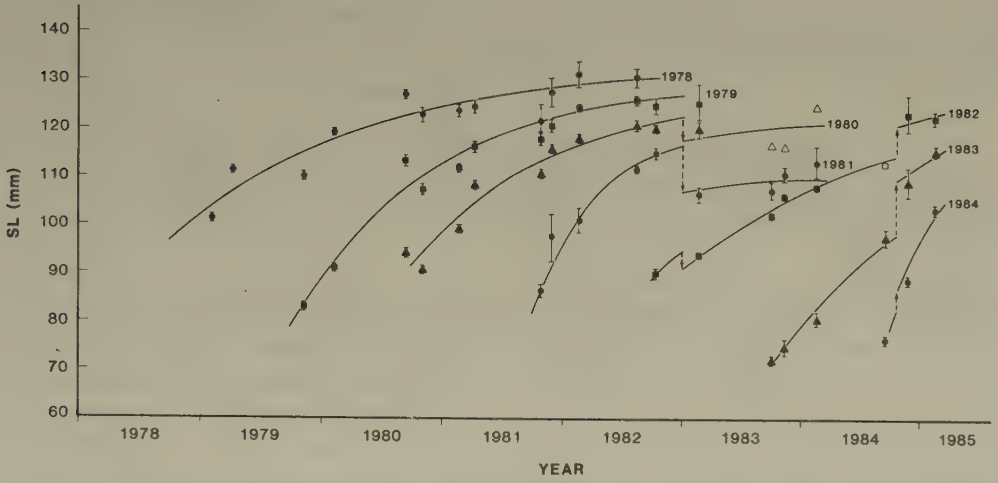

Figure 4. Growth of northern anchovy year classes from DFG age-length data. Von Bertalanfy growth curves are fit to mean lengths (± 2 s.e., except open symbols where s.e. > 5 mm).

(ENSO) events (Fig. 3). Smoothed monthly surface temperature and sea level anomalies since 1925 are highly correlated ($r = +0.71$, $P \ll .001$, sea level record lagged by 1 month). Thus, the temperature record itself provides a good index of El Niño in the Southern California Bight. A notable exception in recent years is the warm anomaly in 1981, which was not associated with a sea level anomaly or an ENSO event.

A northern anchovy recruitment index, equal to the number of recruits in year $t + 1$ divided by the number of spawners in year t, was calculated from data in MacCall and Methot (1983). Reliable recruitment estimates are not available for years prior to 1968. The recruitment index is not significantly correlated with yearly surface temperature anomaly ($r = +0.34$, $P > .05$). There is no simple relationship between recruitment and El Niño in the 17-year record containing three El Niño events and one non-ENSO warm event.

b. Juvenile and adult growth. Figure 4 illustrates growth curves fit to observed mean lengths for 1978–1984 year classes. There are obvious discontinuities between October 1982 and February 1983 and between September and November 1984. Therefore, growth curves were fit to the 1980 and 1981 year-class data before the first break, to the 1982 and 1983 year-class data between the breaks, and to the 1984 year-class data after the second break. Comparison of predicted lengths with the observations not used to fit the curves suggests that 1-, 2-, and 3-year-old fish (1982, 1981 and 1980 year classes) were 3, 10, and 5 mm shorter than expected, respectively, beginning in early 1983. Similarly, 1984, 1983 and 1982 year-class fish underwent sudden increases in length of 4, 11, and 6 mm between September and November 1984.

Table 3. Juvenile lengths and growth rates, on October 1 of birth year, from fitted growth curves in Figure 6. Estimates in parentheses are based on limited data.

	Year Class							
	1978	1979	1980	1981	1982	1983	1984	1985
Length, mm	96.5	78.8	91.7	81.8	89.6	71.2	78.8	(79.4)
Growth rate, mm/yr	91.2	124.5	116.0	261.3	79.4	78.1	(259.2)	—

Growth of 1982 and 1983 year-class fish during El Niño was 13–70% (mean = 47%) slower than growth of 1978–1981 year-class fish at the same age (Table 3). 1982 year-class fish had attained a mean length of only 109 mm as 2-year-olds, in March 1984, compared with 116–120 mm for the 1978 to 1980 year classes (Fig. 4). Juveniles in the 1983 and 1984 year classes were as much as 25 mm shorter than in 1978–1982.

Regional differences in historical mean growth rates and lengths-at-age were revealed by fitting von Bertalanffy growth curves to subsets of 1973–1982 DFG age-length data. Growth rates are higher north of the U.S.-Mexico border (29.8 mm/yr at 100 mm) than to the south (16.9 mm/yr at 100 mm). In these data, there was no difference in asymptotic length to the north and south of the border (133.4 and 134.4 mm, respectively).

During 1978–1982, 1- and 2-year-old fish were ~7 mm shorter south of the U.S.-Mexico border than to the north (Table 4). In February 1983, very few fish were sampled south of the border, but the length of "northern" 1-year-olds was about equal to the normal length of "southern" 1-year-olds. However, northern 2-year-olds were significantly shorter than the 1978–1982 mean for southern 2-year-olds.

c. Spawning range. Figure 5 illustrates 1980–1985 spawning ranges as indicated by distributions of eggs. The cold-water boundary corresponding approximatey to the 14°C isotherm in 1980–1982 (Fiedler, 1983) had moved far to the north in 1983. No surface water <14°C was observed south of Pt. Conception after the first week of February 1983 (GOSSTCOMP sea surface temperature maps, National Environmental Satellite, Data, and Information Service). Anchovy eggs were found much

Table 4. Mean (s.e.) standard length at age (mm) of anchovy caught north and south of the U.S.-Mexico border on DFG winter anchovy acoustic surveys.

		Age, years			
		1	2	3	4
1978–1982	N	99.8 (.35)	119.2 (.25)	126.8 (.29)	134.2 (.72)
	S	93.1 (.63)	112.6 (.52)	122.4 (.66)	122.6 (2.02)
1983	N	94.3 (.31)	107.2 (.84)	120.5 (.86)	126.2 (1.93)
	S	94.9 (1.73)	106.5 (2.16)	—	—

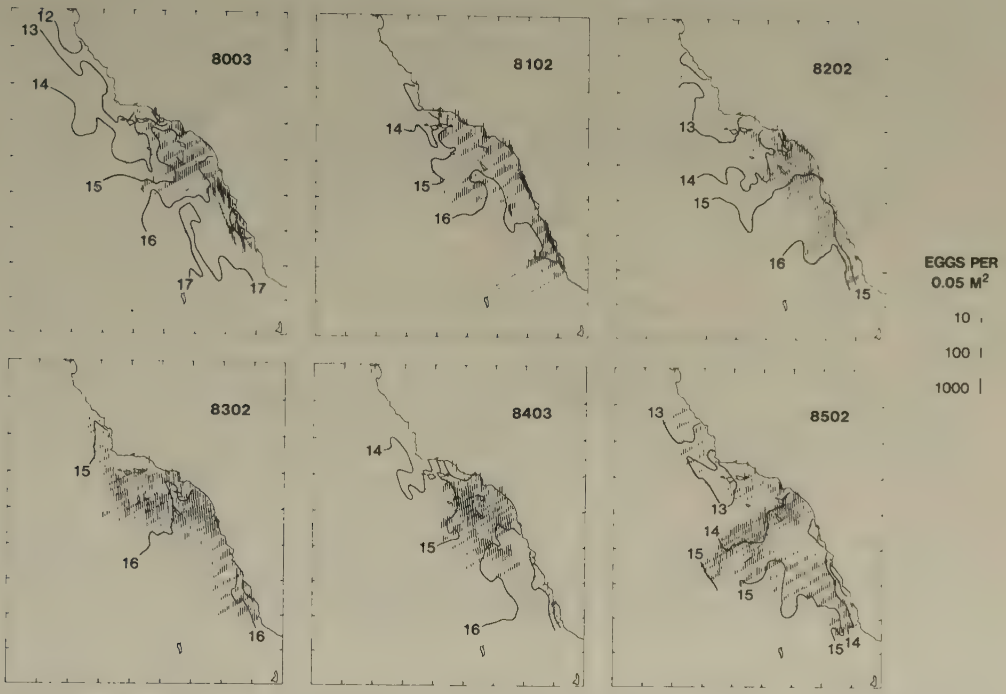

Figure 5. Surface isotherms (°C) and egg distributions on anchovy biomass cruises (CalCOFI 8003-4, 8102, 8202, 8302, 8403, and 8502).

farther north and offshore than in 1980–1982: spawning range increased by 43%, as measured by the area containing 95% of the sampled eggs. In 1984, the cold-water boundary was again present south of Pt. Conception, but spawning continued relatively far offshore. Very few eggs were found in the area off northern Baja California south of Ensenada, but the presence of adults and larvae (Hewitt, 1985) indicates that spawning activity had ceased shortly before sampling. In 1985, scattered eggs were found in 13°C water to the north of Pt. Conception, while large numbers of eggs were found unusually far offshore to the south of the Channel Islands.

d. Larval survival. Figure 6 illustrates survival of anchovy yolk-sac and first-feeding larvae. In every year except 1983, mortality (slope of the survival curves) increases at 4 mm. In 1983, yolk-sac mortality was significantly higher than in other years, and was equal to mortality after feeding began. There were no significant differences in first-feeding mortality among these years (Table 8).

4. Discussion

a. El Niño and other clupeoid stocks. El Niño causes striking biological changes in the eastern equatorial Pacific off Peru and Ecuador. Onshore and poleward transport

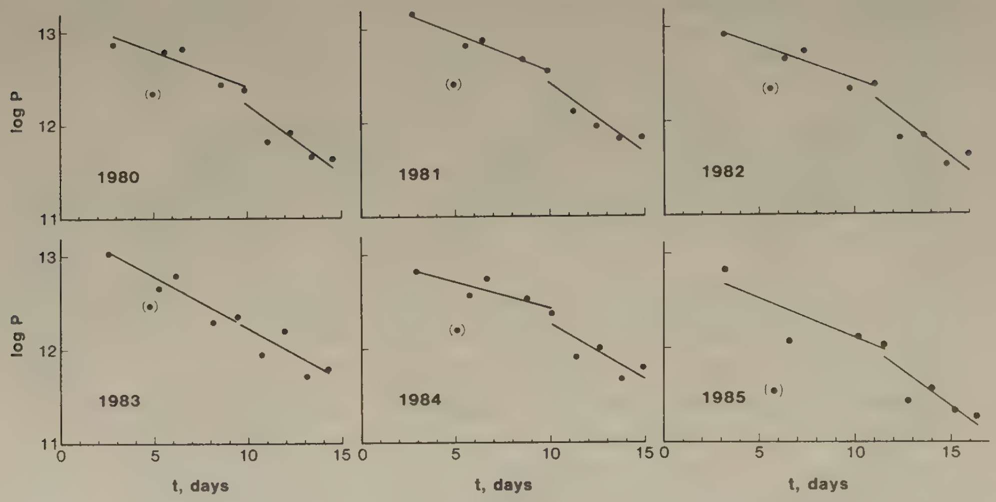

Figure 6. Survival of yolk-sac and first-feeding larvae from CALVET samples. P = daily production of larvae in 0.5-mm size intervals. First point is daily production of hatching eggs. Production of 2.0-mm larvae (in parentheses) was not used in curve-fitting.

of warm surface waters depresses the thermocline/nutricline, reducing the nutrient input from below which normally drives this very productive coastal upwelling ecosystem. Large drops in primary productivity and standing crops at all trophic levels are observed (Barber and Chavez, 1983).

The Peruvian anchoveta fishery was the world's largest for nearly a decade until three successive poor year classes in 1971–1973 decimated the stock. Larval mortality was unusually high in the El Niño years of 1967, 1972, and 1977. Walsh *et al.* (1980) attributed this to the poleward movement of adult spawners into a suboptimal habitat for first-feeding larvae, with low availability of appropriate food organisms and increased abundance of euphausiid predators. Tsukayama and Alvarez (1980) observed reduced size and more variable sexual maturity of adult anchovies in the warm-water years from 1964 to 1978. Santander (1980) observed that egg production was low in 1971–1973 and that spawners were concentrated very near the coast during the 1972–1973 El Niño. They remained extremely vulnerable to the fishing fleet even as the stock declined from low recruitment and overfishing. In this case, a natural environmental perturbation was compounded by overfishing.

The variability of many stocks of short-lived, pelagic, schooling fishes such as engraulids and clupeids has been related to El Niño (Shannon *et al.*, 1984). However, the effects of El Niño are not universally adverse. For example, the sardine (*Sardinops sagax*) actually increased during recent El Niño events, concurrent with the decline of the anchoveta stock (Santander, 1980; Pastor Feria, 1984).

b. California El Niño 1982–1984. El Niño 1982–1983 in the eastern equatorial Pacific has been extensively reported and documented (cf. Cane, 1983; Tropical

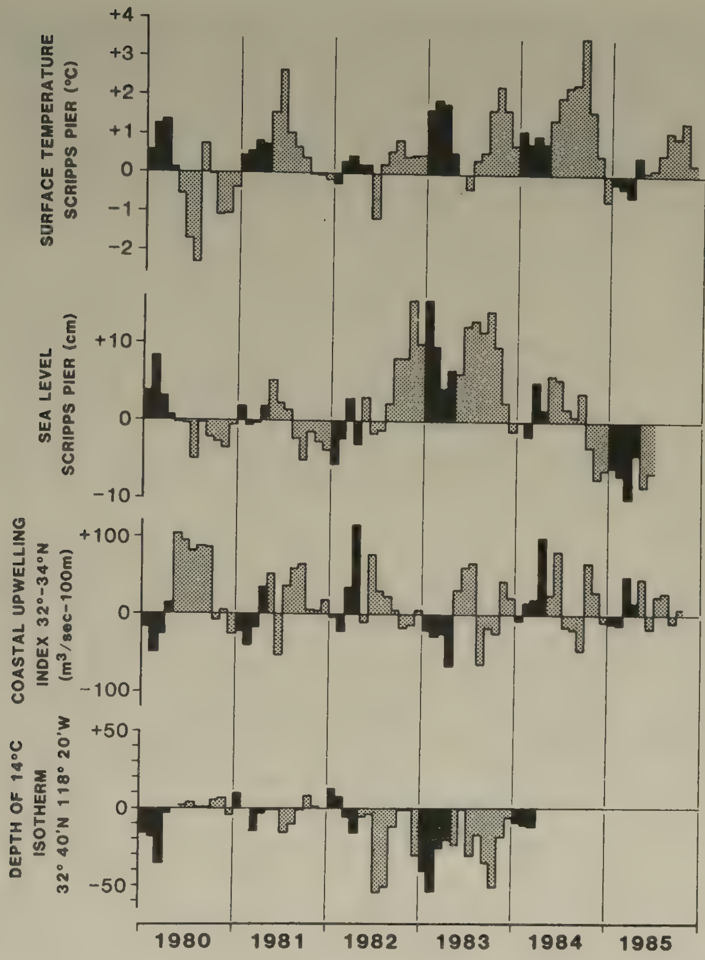

Figure 7. Monthly anomalies of surface temperature and sea level at Scripps Pier, coastal upwelling index in a 3 × 3 degree square at 33N, 119W (A. Bakun, NOAA/NMFS/Pacific Fisheries Environmental Group, pers. comm.), and depth of the 14°C isotherm at 32.7N, 118.2W (D. McLain, NOAA/NMFS/PFEG, pers. comm.). Peak anchovy spawning months, January–April, are solid black.

Ocean-Atmosphere Newsletters 16, 21, 24, and 28). As early as July 1982, anomalies in the structure of the water column off southern California signalled the extension of El Niño into the northeastern Pacific (Fig. 7). The 14°C isotherm is generally in the top of the seasonal thermocline in the Southern California Bight (Lynn *et al.*, 1982), and thus represents the mixed layer depth. A deepened mixed layer and elevated sea level were the first changes observed. Surface temperature changes were significant by January 1983. Large positive anomalies occurred in three successive periods: winter 1982–83, late summer 1983, and summer 1984. During peak anchovy spawning in 1983, surface temperature and sea level at La Jolla were 1.5°C and 9.1 cm above normal. During 1984 spawning, the anomalous conditions had abated somewhat, but the largest surface temperature anomalies occurred later in summer 1984.

The positive sea level anomaly during winter 1982–1983 represents an unusually strong poleward countercurrent along the coast (Lynn, 1983). Offshore Ekman transport (coastal upwelling index) was low in early 1983. Changes in wind-driven flow in the California Current System were caused by large-scale atmospheric perturbations during winter 1982–1983: intensification and expansion of the Aleutian low and reduced strength of the North Pacific high (Simpson, 1984). Finally, the unusually deep 14° isotherm marks the depth of nitrate-depleted surface waters at this latitude (Cullen *et al.*, 1983). Therefore, two sources of exogenous nutrients in Southern California Bight surface waters—advection from the north and mixing from below the nutricline—were diminished during 1983. McGowan (1985) demonstrated that the nitracline, on a transect perpendicular to the coast, 100 km north of San Diego (CalCOFI line 90), was anomalously deep from March to December 1983, coinciding with the deep thermocline.

c. Biological effects of California El Niño 1982–1984. In May 1983, phytoplankton biomass in the Southern California Bight was relatively low (Table 5). Integrated chlorophyll was only 54% of the March–June historical mean (−1.79 standard deviation units, $p \sim .05$). Measured primary productivity was almost twice the rate of 500 mg C m^{-2} day^{-1} predicted from Smith and Eppley's (1982) regression analysis of productivity vs. daylength and Scripps Pier temperature anomaly, adjusted for incomplete coverage of the 16-station SCBS grid in 1983. However, the Scripps Pier temperature anomaly was only +0.01°C in May, compared with +1.49°C in January–April. Equatorward winds that cause coastal upwelling and offshore transport were stronger than normal in May, following four months of unusually low winds. The high productivity of this diminished phytoplankton stock probably reflects a short-term response to the temporary relaxation of warm-water conditions in late spring and early summer 1983 (see Fig. 7).

In March and April, the subsurface chlorophyll maximum layer was up to 70 m deeper than normal beyond ~50 km from the coast (McGowan, 1983). From July through December, the chlorophyll maximum was anomalously deep even near the coast. In late summer 1983, chlorophyll levels in the upper 50 m were as much as an order of magnitude lower than usual (McGowan, 1985). Reduced surface chlorophyll levels during El Niño (Fiedler, 1984a) can be explained in part by the deepened chlorophyll maximum layer. Kelp production off southern California was severely reduced by nutrient depletion during 1983 (Dayton and Tegner, 1984; Zimmerman and Robertson, 1985). Phytoplankton production may have been similarly affected.

Available data indicate that during peak spawning actvity in 1983, El Niño affected the vertical distribution of phytoplankton more than absolute levels of productivity or biomass. Survival of first-feeding anchovy larvae is dependent on a critical density, size

Table 5. Areally-weighted means of integrated euphotic zone phytoplankton biomass, mg chl a m^{-2}, and primary productivity, mg C m^{-2} day^{-1}, at four stations between San Diego and Los Angeles and up to 100 km offshore (stations 101, 202, 205, and 206, Southern California Bight Study, Food Chain Research Group, Scripps Institution of Oceanography). SCBS data from R. Eppley (SIO/FCRG, pers. comm.). CalCOFI data from University of California, Scripps Institution of Oceanography, Physical, Chemical and Biological Data Reports, SIO References 84-25 and 85-14.

Cruise	Dates	Chlorophyll	Productivity
SCBS-3	16–24 June 1975	30.1	1675
SCBS-7	2–9 June 1976	32.4	492
SCBS-16	7–12 May 1980	40.9	416
SCBS-18	5–12 May 1981	24.2	766
SCBS-22	16–25 May 1983	17.3	942
CalCOFI 8404	9–16 April 1984	33.9	—
CalCOFI 8505	1–8 May 1985	47.3	—

range, and species composition of food organisms. Optimal conditions are frequently found in subsurface layers of larger naked dinoflagellates in stratified waters of the Southern California Bight (Lasker, 1981). We do not know of any sampling that was adequate to detect phytoplankton community change in the Southern California Bight during El Niño. However, seasonal and spatial variations of species composition in earlier studies have been linked to environmental conditions characterized as "upwelling" and "nonupwelling." Assemblages correlated with the two sets of conditions are generally dominated by diatoms and dinoflagellates, respectively.

Goodman *et al.* (1984) found a dinoflagellate assemblage correlated with high temperature, a deep chlorophyll maximum layer, and low silicate in the Southern California Bight. These environmental conditions are typical of late summer in most years, but prevailed for much of 1983. If phytoplankton community changes did occur in 1983, they would be expected to favor such a dinoflagellate assemblage. First-feeding larvae actually prefer certain types of dinoflagellates (Scura and Jerde, 1977), which would explain why we did not detect reduced survival of first-feeding larvae in spring 1983.

Smith and Eppley (1982) did not find a significant relationship between total anchovy biomass in the Southern California Bight and estimated annual primary production between 1951 and 1979, although a major decline in biomass, from 1957 to 1961, was associated with the unproductive 1957–1959 El Niño. They did find that zooplankton biomass in the Southern California Bight was positively correlated with estimated primary production. Bernal (1979) found that monthly macrozooplankton biomass off southern California was consistently below the 1949–1969 means from May 1957 through February 1960. At the extreme of this 34-month negative anomaly, in January 1959, zooplankton biomass was only 18% of the long-term monthly mean.

Zooplankton biomass in the Southern California Bight, from Bongo net samples on

Table 6. Median zooplankton biomasses, g/1000 m^3, in CalCOFI region 7, Southern California Inshore, from CALBOBL tows. Large gelatinous organisms were removed from 6 samples in 8502, and only 4 samples in all other cruises combined. 8004 and 8104 medians (*) were significantly greater than the other 6 by Kruskal-Wallis one-way anova.

Cruise	Dates	*N*	Zooplankton biomass
8003	28 Mar–7 Apr 1980	44	186.4
8004	12 Apr–28 Apr 1980	29	833.8*
8102	12 Feb–7 Mar 1981	32	224.6
8104	31 Mar–19 Apr 1981	37	444.4*
8202	27 Jan–9 Mar 1982	31	305.8
8302	9 Feb–20 Mar 1983	32	98.4
8403	16 Feb–14 Mar 1984	32	219.8
8502	19 Feb–1 Mar 1985	25	138.0

early spring egg production cruises, was not significantly lower in 1983 than in 1980–1982 and 1984–1985 (Table 6). However, beginning in April 1983, zooplankton volumes along CalCOFI line 90 in the center of the Bight were significantly lower than 1949–1969 median values (McGowan, 1984, 1985). The greatest anomalies were found in July and August in the normal offshore maximum 100–200 km from the coast. Reduced availability of zooplankton prey may affect the growth of late larvae, juveniles, and adults.

d. Effects on growth. The age-length data indicate unusually slow growth of juvenile anchovies during summer 1983 and 1984. Butler (NMFS/Southwest Fisheries Center, pers. comm.) found that juvenile length, adjusted to an age of 210 days, was 71.9 mm in 1983 and 76.6 mm in 1984, compared with 83.0–83.5 in 1980–1982. This is equivalent to a weight deficit of 36% in 1983. The most problematic signals in the growth curves are the discontinuities in early spring 1983 and late summer 1984. A distributional shift of the central stock during El Niño, along with regional variability within the stock, may have contributed to the sudden changes in size-at-age. Many warm-water and tropical species appeared off California during El Niño, beyond the normal limits of their ranges (Lea, 1984). Parrish *et al.* (1985) analyzed age-length data from DFG trawls between 1966 and 1983. Mean length of two-year-olds increases from 104 mm in Sebastian Viscaino Bay (central Baja California, 28N) to 120 mm in Santa Barbara Channel (34N). Within the Southern California Bight, mean length increases by 7–8 mm from shallow, nearshore waters to the offshore limits of the stock's range.

Given the latitudinal and onshore-offshore clines in length-at-age, trawls on NMFS biomass surveys suggest that smaller anchovies moved into the DFG survey area from the south during El Niño, while larger fish moved out of the area, to the north and west of Pt. Conception. February 1983 (and 1985) trawls caught anchovies up to the limit of sampling at Morro Bay (35.5N). In 1980–1982 and 1984, no anchovies were caught between Pt. Conception (34N) and Monterey (36.5N). Spawning females caught north of Santa Barbara (34N) in 1983 had a mean weight of 12.9 g, which is greater than the unusually low overall mean of 11.2 g and close to the 1980–1985 anti-El Niño range of 13.4–18.8 g (Table 1). However, an influx of small southern fish cannot entirely explain the changes in length-at-age during El Niño: 2-year-olds in the Southern California Bight in 1983 were shorter than normal 2-year-olds south of the U.S.-Mexico border.

Adult northern anchovy in the Southern California Bight, including probable immigrants from the south, grew significantly slower than normal in 1983. Environmental conditions that may have limited growth in the Southern California Bight during El Niño, such as temperature and plankton biomass, were similar to normal conditions in coastal waters further south. The reduced growth rates of 1982 year-class fish as adults, and juvenile fish during summer 1983 and summer 1984, were most likely caused by El Niño's impact on the availability of appropriate zooplankton prey. We have seen no data on taxonomic changes in the zooplankton community during this El Niño event. Colebrook (1977) found that during the last major California El Niño of 1957–1959, the biomasses of all important taxonomic groups were reduced in 1958 and 1959, relative to 1956–1957.

e. Effects on spawning. Table 7 summarizes central stock spawning activity from 1980 to 1985. Spawning effort by a multiple spawner like the northern anchovy is the number of eggs produced per unit spawning biomass in one spawning season, or daily specific fecundity times the duration of the spawning season. Estimates of spawning season duration are not readily available, although birth-date analysis of 1983 year-class recruits show peak occurrence from February to April, similar to previous years (Methot, 1983; Butler and Methot, unpubl. data). Parrish *et al.* (1986) found that duration of peak spawning activity increases somewhat with age. We estimated the effect of age composition on spawning duration using their monthly mean age-specific spawning activities and the two extremes of age distribution observed during the 1980–1985 period: in 1982, 79% of spawning activity would be expected in February–April, while in 1983, 82% would occur during that peak spawning period. We assume there were no significant changes in duration of spawning from 1980 to 1985 and that specific fecundity, measured on a 4–8 week biomass survey, is a valid measure of relative spawning effort by the stock during peak spawning.

Specific fecundity was low in 1983 and high in 1984, compared with 1980–1985 anti-El Niño years (Table 7). Two important components of specific fecundity may determine changes: batch size (batch fecundity) per unit weight and frequency of production of batches (spawning incidence). The variation in specific fecundity during 1980–1985 is more closely related to variation in spawning incidence ($r^2 = 0.50$) than to variation in fecundity per unit weight ($r^2 = 0.00$).

Batch fecundity was lower in 1983–1984 than in 1980–1982 and 1985. Most of this

Table 7. Northern anchovy central stock spawning parameter estimates, 1980–1985, from Stauffer and Picquelle (1980, 1981), Picquelle and Hewitt (1983, 1984), Hewitt (1985), and Bindman (1985). Batch fecundities for a standard 14.95-g female from Hunter *et al.* (1984) and Lo (NOAA/NMFS/Southwest Fisheries Center, pers. comm.). Coefficients of variation in parentheses, except in 1983 when large-scale geographic variations were noted and the analysis was stratified to reduce the variance of the final estimates.

	1980	1981	1982	1983	1984	1985
Spawning female weight, g	17.50	13.37	18.83	11.20	12.02	14.49
	(.055)	(.039)	(.019)		(.038)	(.022)
Female fraction	.475	.501	.472	.549	.582	.609
	(.120)	(.063)	(.047)		(.053)	(.032)
Batch fecundity observed, at 14.95 g	7788	8208	10845	5297	5485	7343
	(.075)	(.052)	(.038)		(.057)	(.046)
	6423	9237	9055	7870	7640	8234
	(.064)	(.022)	(.025)	(.034)	(.033)	(.030)
Spawning incidence, day^{-1}	.145	.106	.120	.094	.160	.120
	(.125)	(.122)	(.081)		(.132)	(.129)
Specific fecundity, eggs/day-g	30.28	33.03	32.53	24.35	42.43	37.00
	(.197)	(.152)	(.103)		(.132)	(.142)
Egg production, 10^{12} eggs/day	26.34	20.96	13.51	17.25	12.98	16.95
	(.101)	(.111)	(.237)		(.122)	(.156)

change seems to have been caused by reduced spawning female weight. Normalized batch fecundities for a standard size female were slightly low in 1983–1984, but the 1980 value was even lower. Spawning female weight in 1983 and 1984 was reduced due to younger age structure, reduced size-at-age and, perhaps, early sexual maturation. The 1983 stock was relatively young, but mean age was near normal in 1984 (Table 1). We have shown that the size-at-age of spawners was reduced in 1983 and 1984. A relatively large proportion of small fish were sexually mature in 1983 and 1984 (John Hunter, NMFS/Southwest Fisheries Center, pers. comm.). Although these fish were not aged, their size was typical of one-year-old fish.

Spawning incidence was relatively low in 1983 and high in 1984. Parrish *et al.* (1986) found that spawning incidence is strongly age-dependent. Although 1983 had the youngest mean age (Table 1) and lowest spawning incidence (Table 7), we note no correlation between mean age of spawners and spawning incidence in 1980–1985 ($r^2 = +0.07$). Regional variability and changes in stock composition caused by a northward shift cannot explain the low spawning incidence in 1983. Picquelle and Hewitt (1984) found greater specific fecundity in the south than in the north. Reduced spawning incidence and specific fecundity in 1983 was caused by the unusually young age structure of the stock, compounded by small size-at-age.

The high spawning incidence and specific fecundity in 1984 are surprising, because growth of the 1984 spawners had been slow during 1983. Spawning effort during the peak spawning season is supported by fat stores accumulated in early summer of the preceding year (Hunter and Leong, 1981). It seems unlikely that fat storage could be normal while somatic growth, especially of the recruiting 1983 year class, was reduced. The presence of anchovy larvae and spent females, but no eggs, at the southern end of the spawning range in the latter half of March suggests that the spawning season was abbreviated in 1984. Perhaps the high spawning effort could not be sustained due to low fat stores. The high spawning incidence may be a compensatory response to the low spawning biomass in 1984, but the mechanism for such a response is unknown.

Variation in the stock's total egg production was not related to the specific fecundity of the spawners. Total egg production was not reduced in 1983, despite the low specific fecundity, because recruitment of the moderately strong 1982 year class had increased spawning biomass. Total egg production decreased in 1984 when the exceptionally high spawning effort was not sufficient to compensate for the low spawning biomass.

f. Effects on larval mortality. We observed a consistent increase in larval mortality at the size when yolk-sac absorption and initiation of feeding activity are expected to occur, except in 1983 when mortality of yolk-sac larvae was unusually high. Nighttime avoidance of the CALVET net is conceivable and would contribute to the apparent increased mortality of active, first-feeding larvae. Lo (1986) analyzed larval survival to 20 days in 1.0-mm size intervals from CALBOBL sample counts. She used a survival model with a mortality rate that decreases with age after hatching (B = mortality · age, Table 8). The high mortality coefficient for larvae up to 20 days old in 1983 probably reflects the high yolk-sac mortality detected in the present analysis of CALVET samples. We could not describe CALVET sample counts in 0.5-mm size intervals with such a model, perhaps because the CALVET net is a less efficient sampler of large larvae and CALBOBL counts require large corrections for extrusion of small larvae (Lo, 1983).

The most important cause of mortality of yolk-sac larvae is predation (Blaxter and Hunter, 1982). Starvation cannot occur unless an inadequate yolk supply in poor quality eggs is exhausted before development has proceeded far enough to allow feeding activity. In this case, larval production at some size <4 mm would apparently increase as yolk was exhausted and growth slowed, but would subsequently drop as these larvae succumbed to starvation or predation. We observed no such pattern in the 1983 larval abundance data. Increased predation is the most reasonable explanation for the abnormally high yolk-sac mortality in 1983. Cannibalism may have been one

Table 8. Daily production of eggs and 8-mm larvae (10^{12}/day), and intervening egg and larval mortalities (day^{-1}, standard error in parentheses), 1980–1985. 2-8mm larval mortality coefficients (= mortality · age, dimensionless) and larval production from Lo (1985 and pers. comm.).

	1980	1981	1982	1983	1984	1985
Egg production	26.34	20.96	13.51	17.25	12.98	16.95
Egg mortality	.39	.13	.17	.23	.23	.29
	(.10)	(.16)	(.26)	(.29)	(.09)	(.17)
Yolk-sac mortality	.077	.082	.074	.110	.055	.084
	(.011)	(.005)	(.008)	(.013)	(.010)	(.014)
First-feeding mortality	.150	.147	.159	.112	.120	.151
	(.024)	(.018)	(.025)	(.025)	(.022)	(.025)
2-8mm larvae mortality	1.22	1.53	1.81	2.05	1.47	2.13
	(.031)	(.032)	(.036)	(.110)	(.153)	(.103)
8mm larvae production	0.22	0.19	0.20	0.13	0.26	0.13

cause of high predation mortality, but the adult population was small compared to historical levels and there is a great variety of other potential larval predators in the Southern California Bight.

Yolk-sac anchovy larvae are vulnerable to capture by calanoid copepods and euphausiids in the laboratory (Lillelund and Lasker, 1971; Theilacker and Lasker, 1974). No data are available on changes in the abundance of these predators during El Niño 1982–1984, but Colebrook (1977) found that the biomass of these taxonomic groups was reduced during the 1957–1959 El Niño in the California Current.

One exotic and voracious predator did appear off southern California during 1983 and 1984—the pelagic phase of the red crab, *Pleuroncodes planipes*. Large numbers of these organisms were occasionally caught in midwater trawls and CALBOBL tows (Smith, 1985b) and stranded on southern California beaches. *Pleuroncodes* can feed as a visual predator, or in a filtering mode by swimming to the surface, spreading the thoracic limbs, and sinking slowly while grazing larger phytoplankton and microzooplankton (Longhurst *et al.*, 1967). Weakly mobile yolk-sac larvae would be particularly vulnerable to this feeding mechanism. Although we have no direct evidence that *Pleuroncodes* was an important larval anchovy predator in the Southern California Bight during 1983, extremely high predation rates on eggs and yolk-sac larvae have been observed in the laboratory (10–40 liters filtered per day, Gail Theilacker, NMFS/Southwest Fisheries Center, pers. comm.).

Production of 8-mm larvae, the net result of spawning and survival of eggs and early larvae, was relatively low in 1983 and 1985 (Table 8). Anomalous offshore transport by a displaced offshore eddy may have affected apparent larval survival in 1985 (Fiedler, in prep.). Central stock larval production and mortality estimates by Hewitt (1982) indicate that production of larvae at 14 days after hatching (~8 mm) ranged between 0.16 and 0.25 × 10^{12}/day from 1962 to 1979, with two exceptions: 1963 (0.45) and 1978 (0.11). In spite of low larval production, the 1978 year class was the largest observed since reliable estimates began in 1968. This illustrates an important caveat for fisheries recruitment studies limited by the paradigm that survival of early life history stages is the sole determinant of year-class strength. Despite variability in survival and growth of eggs and early larvae, survival of late larval and juvenile stages may ultimately determine the successful recruitment of a particular year class in some stocks.

5. Summary and conclusions

Data from a variety of sources show that the temperature and structure of the surface layer, surface currents, and upwelling intensity in the anchovy habitat off southern California were altered during El Niño 1982–1984. Total phytoplankton biomass was slightly reduced in spring 1983, but availability of food organisms in surface waters may have been further reduced by the extreme deepening of the chlorophyll maximum layer. Macrozooplankton biomass was significantly less than normal for most of 1983.

Distribution of the anchovy stock apparently shifted to the north in 1983, along with sea surface temperature boundaries. Spawning range expanded. Specific fecundity was low in 1983 due to an unusually high proportion of young females in the spawning stock. Yolk-sac mortality was abnormally high in spring 1983, most likely caused by predation. Growth of juveniles and adults was significantly slowed during 1983, probably due to reduced availability of zooplankton prey. Spawning effort in 1984 was high, so that reproductive output was normal in spite of the reduced size and abundance of spawning females.

Low recruitment in 1983 was caused by a combination of factors: low specific fecundity, high mortality of yolk-sac larvae, and possibly high predation pressure on juveniles due to an influx of scombrid predators from the south (Bernard *et al.*, 1985). By February 1985, length-at-age and stock size had returned to pre-El Niño levels, due to strong recruitment of the 1984 year class. The northern anchovy population has undergone large fluctuations in the past and yet continues to persist. We expect that the anchovy will continue to experience and respond to the low-frequency environmental perturbations characteristic of eastern boundary current systems.

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SIZE-SPECIFIC VULNERABILITY OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE TO PREDATION BY FISHES

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ABSTRACT

Vulnerability of larval northern anchovy (6-33 mm SL) to predation by adult northern anchovy and juvenile chub mackerel, *Scomber japonicus*, was estimated by measuring the response and escape probabilities of larvae. The proportion of larvae responding to the attacks of either predator increased with larval length and differed little between predator species. About 20% of 6 mm larvae responded to attacks of predators while 85-100% of 33 mm larvae responded. The proportion of larvae escaping attacks also increased with larval length, but more larvae of all sizes escaped the attacks of adult northern anchovy than those of juvenile chub mackerel. The rate of consumption of northern anchovy larvae by adult northern anchovy was highest when the larvae were 8.5-15 mm long, indicating that greater avoidance success of larvae in this size range relative to smaller ones may not completely compensate for their greater visibility to predators.

The events that cause variation in year-class strength in marine fish stocks occur during the first year of life, but no single life stage or period has been identified as being uniquely influential in the establishment of year classes. Mortality rates are size specific over this period with rates being the highest during the egg and yolk-sac stages and declining thereafter (Hunter 1984; Smith 1985). Variation in the relatively low mortality rates of older larval and juvenile stages may be more influential in year-class formation than the variation of the high mortality rates of eggs and first feeding larvae (Smith 1985). Thus all early life stages from egg through juvenile must be considered and knowledge of the size- or age-specific vulnerability of larvae to predation and starvation is central in any attempt at modeling the recruitment process.

Starvation is probably a direct source of larval mortality for only a few weeks after the onset of feeding, and most losses in the first year of life may be attributed to predation. Predation is believed to be the major cause of mortality during the egg and yolk-sac stages (Hunter 1984), and incidence of starving jack mackerel, *Trachurus symmetricus*, and northern anchovy, *Engraulis mordax*, in the sea indicate that significant starvation mortality is restricted to the first 1-2 wk of feeding or about 10-20% of the larval period (O'Connell 1980; Hewitt et al. 1985; Theilacker 1986). The vulnerability of larvae to predation has been studied over limited size ranges; laboratory data indicate that yolk-sac larvae seem to be vulnerable to small invertebrate predators (copepods, amphipods, and euphausiids [Hunter 1984]). In addition, some egg and larval predators have been identified in field studies and in several cases loss rates due to predation have been estimated (Möller 1984; Frank and Leggett 1984; Van der Veer 1985; Purcell 1985; older literature summarized by Hunter 1984).

The objective of this paper was to determine the size-specific vulnerability of northern anchovy larvae to predation by pelagic fishes. The size-specific vulnerability of larval Cape anchovy, *E. capensis*, to cannibalism has been investigated by Brownell (1985) and vulnerability of larval *E. mordax* to predation by the aquarium fish *Amphiprion percula* was studied by Webb (1981). The results of the current study will be compared to these papers in the discussion.

Our approach was to observe the avoidance behavior of northern anchovy larvae in response to predatory attacks by adult northern anchovy and juvenile chub mackerel, *Scomber japonicus*. Adult northern anchovy were selected as a predator because it is the most abundant fish stock in the California Current region and because it has a planktivorous diet which includes fish eggs and larvae (Baxter 1967; Hunter and Kimbrell 1980). Chub

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mackerel is also a major fish stock in the region and is both planktivorous and piscivorous, with juvenile and adult northern anchovy being a dominant item in the diet of larger individuals (Schaefer 1980; Hunter and Lynn, unpubl. data, Southwest Fisheries Center, La Jolla, CA).

MATERIALS AND METHODS

Experimental Fishes

The northern anchovy larvae used in the experiments were reared from the egg; 2,000-7,000 eggs, from a laboratory brood stock (Leong 1971), were stocked in 400 L black circular fiberglass tanks containing about 150 L of filtered seawater. The culture methods of Hunter (1976) were used to rear the larvae, with extra additions of wild zooplankton when the larvae were 10-25 mm SL. Temperature in the rearing tanks was maintained at about 18°C (range, 17.2°-19.2°C).

Three groups of 5 adult northern anchovy (range of mean standard length [SL] = 8.3-8.9 cm) and a single group of 3 juvenile chub mackerel (mean SL = 19.1 cm) were used as predators. They were fed mainly adult brine shrimp and occasionally northern anchovy larvae. The predators were not fed for 10 h before an experiment.

Apparatus

Predators were kept in two rectangular fiberglass tanks ($0.75 \text{ m} \times 2.15 \text{ m} \times 0.83 \text{ m} = 1.35 \text{ m}^3$) with a clear glass window on one side for observation. Two 100 W tungsten household lamps produced 2,000-3,000 mc at the surface of each tank and a black plastic tent enclosed the window, providing a darkened compartment for an observer. Larvae were released into the tank by gently submerging a beaker at the water surface. Horizontal and vertical metric scales on the tank window aided estimation of predator attack distances. The tanks were continuously supplied with ambient seawater ranging from 20.5° to 23.8°C, except during an experiment when the water was static.

Experimental Procedure

It was necessary to measure the feeding performance of predators fed a standard prey because 1) adult northern anchovy are easily frightened and fright behavior reduces feeding motivation; 2) feeding could be affected by satiation during an experiment; and 3) feeding could be affected by the fish learning and responding to cues associated with the introduction of food. We used live adult brine shrimp (*Artemia* sp., 6.4 mm mean total length, standard deviation [SD] 1.2 mm, $n = 25$) as a standard prey. Variation in feeding performance of the predators could be more easily detected when *Artemia* were used because unlike the larvae the *Artemia* did not vary in size among experiments nor did they avoid attack by the predators.

Northern anchovy larvae and the adult *Artemia* were added to the tank in groups of three. An addition of three of either prey constituted a trial. A trial ended after 5 min or when all prey were taken. During a trial we used a computer compatible event recorder to record observations of the interactions between predator and prey. All the experiments using northern anchovy as predators started with 5 consecutive trials in which 3 *Artemia* were offered per trial. This was done to insure that northern anchovy predator groups had a similar level of feeding motivation. Preliminary experiments indicated that it normally took a few feeding trials before adult northern anchovy fed consistently. After the 5 initial trials, predators were offered fish larvae and adult *Artemia* alternately for 4-10 trials. Adult *Artemia* were always used in the last trial to determine if satiation had occurred. A less rigorous schedule was used for the chub mackerel predators because their feeding behavior was less variable than that of the northern anchovy. After 3 initial *Artemia* trials, the chub mackerel were given 5 larval trials followed by an *Artemia* trial. In most cases, a second set of 5 larval trials were also given and these were followed by a final *Artemia* trial to check if satiation had occurred.

The number of observations for each larval size class was the total number of predator-prey interactions observed among larvae in that size class. This number exceeded the number of larvae tested in many cases because, if a larva escaped the first encounter with a predator, the subsequent encounter was also recorded as an event. The total number of observations (predatory events) per larval size class (mean SL), when northern anchovy were the predators, was 5.9 mm, 24; 8.5 mm, 55; 11 mm, 48; 15 mm, 53; 21 mm, 82; and 33 mm, 62. Those for the chub mackerel experiments were 6.7 mm, 19; 10 mm, 75; 16 mm, 54; 21 mm, 27; 31 mm, 47; and 50 mm, 39.

Classification of Behavior

Prey behavior was recorded only when the predator attacked a prey. An attack was defined as a movement directed toward the prey with the mouth open. During an attack the northern anchovy predator usually increased its swimming speed, but the chub mackerel increased speed only when attacking larvae larger than 10 mm SL.

Four measures of predator-prey interactions were calculated: mean and maximum attack distance; frequency of avoidance responses; frequency of escapes; and predation rate (percentage of larvae captured during the 5-min trials). The attack distance was the distance in decimeters (dm) from the prey to the point where the predator started the attack. An avoidance response was a change in speed or direction of a larva occurring before the predator had completed the attack by closing its mouth.

An escape was defined as a larval response in which the predator failed to capture the larva during a single attack. Repeated attacks were scored as separate events. By definition, adult *Artemia* could not be credited with an escape since they did not respond to an attack. Cases where attacked *Artemia* were not captured were considered predator errors. Predator error could only be assessed for *Artemia*. All interactions between predators and larvae in which the larvae were not captured were recorded as an escape.

Predator Performance

The feeding success and variation in feeding rates of predator groups fed live adult *Artemia* were analyzed to estimate predator error and to determine if differences existed in feeding performance among predator groups, or among or within experiments. An experiment was 2-5 larval trials conducted on a single size class of larvae on one day using a single predator group.

Predator errors were obvious when *Artemia* were the prey because *Artemia* did not avoid the attack. In such cases the trajectory of the attack was inaccurate and the predator simply missed the prey. Such errors occurred in 3.4% of the attacks on *Artemia*; this estimate is similar to error rates estimated for other predators (Curio 1976). We could not measure the predator error when larvae were the prey because we attributed any failure to capture a larva to larval avoidance success. Presumably our estimates of larval escape probabilities include an unknown number of cases where failure to capture a larva was the direct result of inaccuracies in the predator's attack rather than being the result of larval avoidance.

Considering all northern anchovy predator groups, predator error in capturing *Artemia* was higher in the first 5 trials than in the subsequent trials of the experiments where *Artemia* trials were alternated with larval trials (Fig. 1A). Predator error averaged 3.4% for all *Artemia* trials, whereas it was 2.1% during the period of alternating larval and *Artemia* trials. Similarly, adult northern anchovy took more time to capture all the *Artemia* in the first trial than in subsequent ones (Fig. 1B). No decline in feeding performance on *Artemia* existed at the end of the experiments, indicating that satiation did not constitute a bias in the experiments. The initial decline in the time required for northern anchovy predators to capture *Artemia* may have been caused by an increase in feeding motivation, learning, or a decrease in fright behavior. As the decline occurred during only the initial 5 *Artemia* trials, the larval data were probably unaffected.

Minor differences in feeding performance also existed among predator groups. In two experiments northern anchovy predatory groups fed markedly less on both *Artemia* and larvae (30% fewer prey taken in 5 min; *t*-test, $P < 0.05$). The effect of omitting these two experiments is indicated in the results. Overall, comparisons of feeding performance among groups, within trials, and among experiments indicated that variation in predator performance as measured by predation rates on *Artemia* was not significantly biased (additional details are given by Folkvord 1985) (see also Figure 1).

RESULTS

Probability of a Response to Predators

The most striking feature of the vulnerability of the youngest larval stages of northern anchovy to predators was the low frequency of escape attempts. Only 16% of the 6 mm larvae responded to the attacks of northern anchovy predators (Fig. 2B) and only 26% of 6.7 mm larvae responded to chub mackerel predators (Fig. 3B). The probability of smaller larvae (SL <20 mm) responding to either chub mackerel or northern anchovy predators was about the same (Fig. 4), although size, feeding behavior, and body form of these two fishes were distinctly different. The tendency to respond to attacking predators steadily increased with larval size until by the time northern anchovy larvae were 30 mm all attempted to avoid attacking northern anchovy and over 80% responded to chub mackerel attacks.

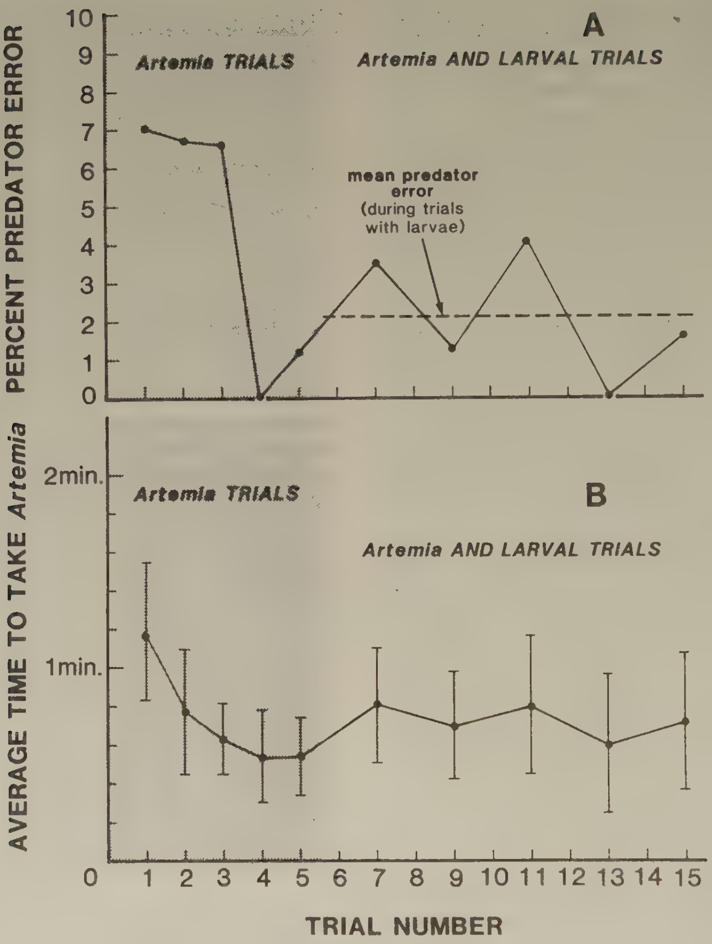

FIGURE 1.—Variation in feeding performance of northern anchovy predators fed live *Artemia* as a function of trial number (equivalent to elapsed time of experiment); shaded area indicates trials in which northern anchovy were fed only *Artemia*; unshaded areas, *Artemia* trials alternated with larval trials. A, percent predator error in capturing adult *Artemia* (percentage of attacks in which a northern anchovy missed the prey); dashed line indicates mean. B, mean time required for predator group to capture 3 adult *Artemia*; bars are 2 × SE of the mean. (*N* = 21.)

Success of Avoidance Movements

Larval vulnerability depended not only on the responsiveness but also on the success of avoidance movements. The proportion of larvae escaping northern anchovy predators increased from 8% for 6 mm larvae to 92% for 33 mm larvae with an estimated 50% of the 17 mm larvae escaping. The percentage of larvae escaping the attacks of chub mackerel was lower than for adult northern anchovy, but the curves given in Figures 2 and 3 had a similar form. Weibull curves were fit to the data to provide trend lines (equations and parameters given in Figure legends). The fraction of larvae that escaped increased from 6% of 6.7 mm larvae to an estimated 50% of the 30 mm larvae. Of the 50 mm juvenile northern anchovy used as prey only 64% escaped the attacks of the chub mackerel.

The ability to successfully avoid predator attacks was strongly affected by species-specific differences in predator behavior since the fraction of larvae escaping the attacks of northern anchovy increased much more rapidly with larval length than did the fraction escaping the attacks of chub mackerel. In contrast, the fraction of smaller larvae (SL <20 mm) responding to the attacks of these two predators was similar (Fig. 4). This indicates that probability of a larva responding to an attack is less affected

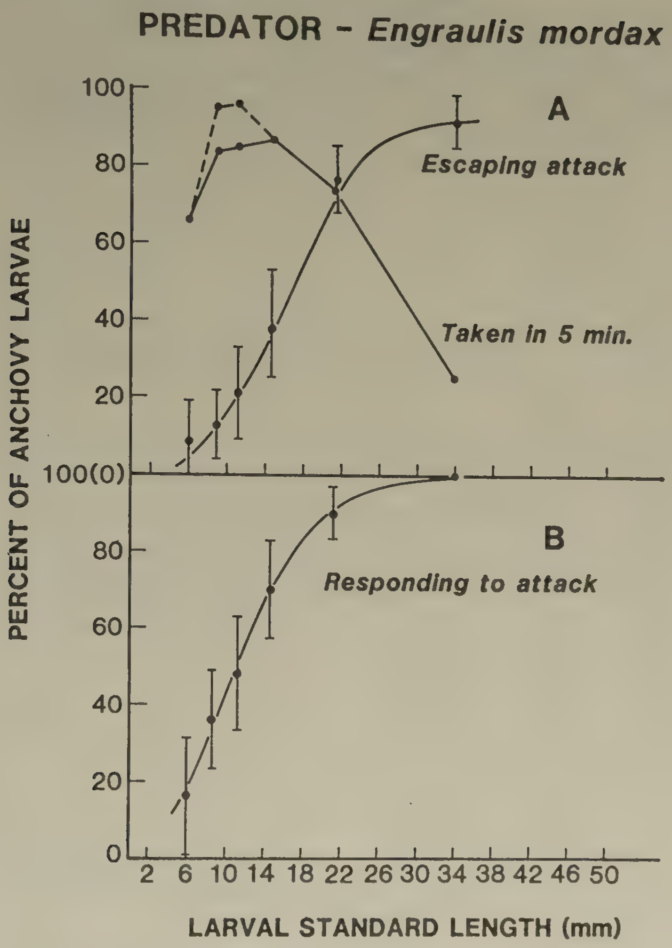

FIGURE 2.—Vulnerability of northern anchovy larvae to adult northern anchovy predators as a function of larval length. A, Percentage of northern anchovy larvae escaping attack; bars are 2 × SE; line is Weibull curve fit to six points using Marquardt's least squares method (Pielou 1981); equation is $N = K(1 - \exp(1 - (L/b) - \lambda))$ where $K = 0.93$, $b = 17.85$, $\lambda = 2.85$, N is the percentage of larvae and L = larval length; and predation rate of the northern anchovy predators (percentage eaten in 5 min) where dashed line is data when experiments with biased predator feeding motivation are omitted. B, Percentage of northern anchovy larvae that responded to the attack of an adult northern anchovy; bars are 2 × SE; and Weibull parameters for curve are $K = 1.00$, $b = 13.58$, and $\lambda = 1.94$.

by differences in predator behavior than is its success in avoiding the attack.

The success of avoidance movements can be separated from larval responsiveness by calculating the avoidance success of responding larvae (numbers escaping/numbers responding). Webb (1981) found no change in this fraction over the larval size range he examined (3-12 mm SL), indicating that changes in responsiveness alone were responsible for the decline in the vulnerability of northern anchovy larvae to *Amphiprion* with increasing larval length. In the present study, no significant trend existed in the success of avoidance movements over the size range of larvae studied by Webb (1981) but success of avoidance movements greatly increased in larger larvae (Fig. 5). The figure also indicates that northern anchovy larvae were much more successful in avoiding *Amphiprion* than in avoiding adult northern anchovy and that the larvae had the least success in avoiding chub mackerel.

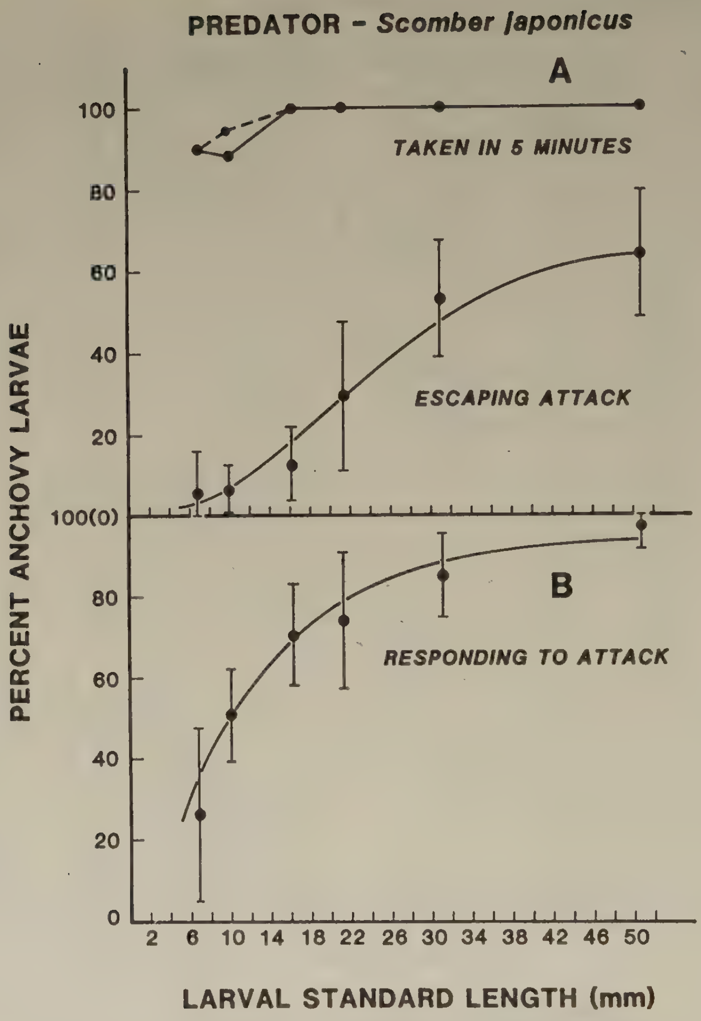

FIGURE 3.—Vulnerability of northern anchovy larvae and juveniles to juvenile chub mackerel predators as a function of anchovy length. A, percentage of northern anchovy larvae escaping attack; bars are 2 × SE; line is Weibull curve fit to six points using Marquardt's least squares method (Pielou 1981); equation is $N = K(1 - \exp(1 - (L/b) - \lambda))$ where $K = 0.66$, $b = 27.41$, N = percentage of larvae, L = larval length, and $\lambda = 2.12$; and predation rate of chub mackerel predators (percentage eaten in 5 min) where dashed line is data when experiments with biased predator feeding motivation are omitted. B, percentage of northern anchovy larvae that responded to the attack of a chub mackerel, bars are 2 × SE; and Weibull parameters for curve are $K = 0.93$, $b = 12.61$, and $\lambda = 1.24$.

Predation Rates

The predation rate of northern anchovy (proportion of larvae consumed by northern anchovy predators in 5 min) reached a maximum somewhere between larval lengths of 8.5 and 15 mm when all data were used, but it occurred between larval lengths of 8.5 and 11 mm when we deleted the experiment where northern anchovy predator performance was lower than average (dashed line in Figure 2A). Statistical comparisons of the fraction of larvae consumed in the various size classes indicated that 6.8 mm larvae were taken less often than larvae in 8.5, 11, and 15 mm size classes despite the fact that these larvae had a low escape ability ($P < 0.05$; normal approximation to the binomial mean; n = 35, 48, 40, and 60, for 5.9, 8.5, 11, and 15 mm size classes). Owing to their small size and

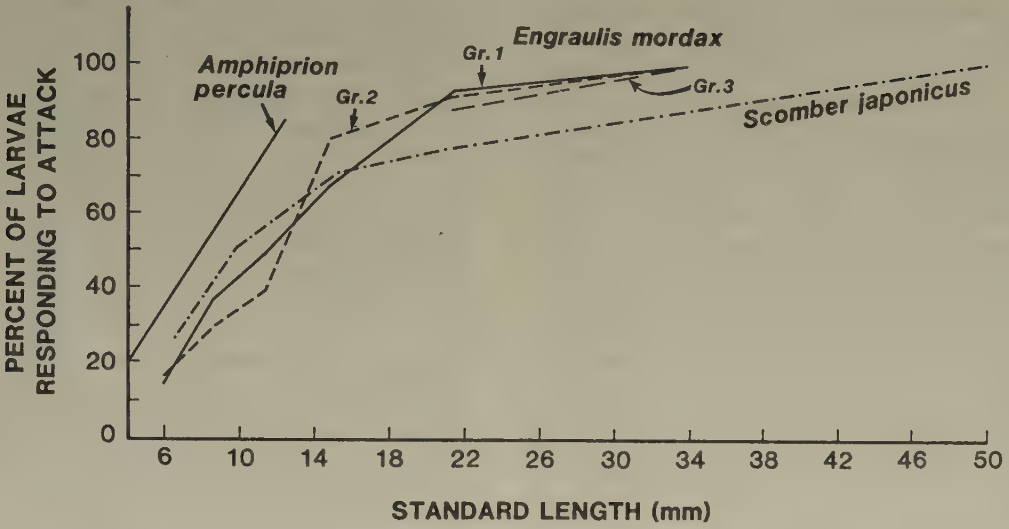

FIGURE 4.—Percentage of northern anchovy larvae that responded to attacks by adult northern anchovy (lines for the three different predator groups shown separately), chub mackerel and the aquarium fish *Amphiprion percula* (from Webb 1981).

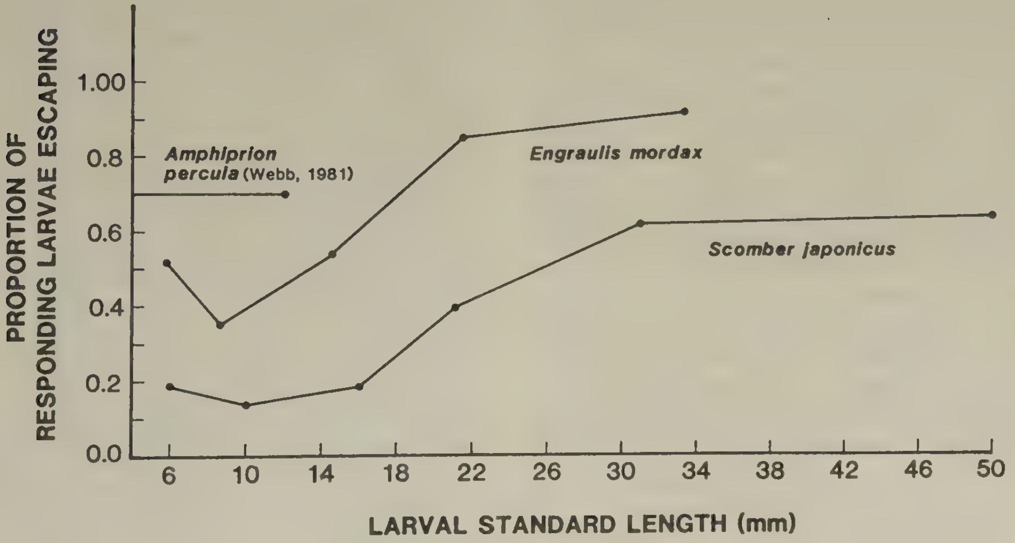

FIGURE 5.—The percentage of responding northern anchovy larvae in various length classes that escaped the predator. Species names identify the predator species.

lack of pigmentation, 6 mm larvae may have been less visible to the predators than larger larvae and consequently were detected less frequently. The decline in predation rates in larvae longer than 15 mm was the result of their greater escape ability.

The number of larvae consumed in 5 min was an insensitive measure of predation rates of chub mackerel, because they usually ate all larvae in the tank within 5 min regardless of their size. Only in the two smallest larval size groups (6-10 mm SL) were some larvae left after a 5-min elapsed time; the deletion of one experiment because of low chub mackerel predator performance changed the predation rate on 10 mm larvae from 87 to 95% (dashed line in Figure 3A). These adjusted data indicate that the feeding rate of chub mackerel was lowest when the smallest larval size group (6.7 mm) were the prey.

Predator Behavior

Sighting distances, persistence of the attack, attack speed, and other characteristics of predator behavior were not well documented in our experiments because our focus was on the larvae. Such information could be quite useful if one were to develop a predation model for northern anchovy larvae, using northern anchovy or chub mackerel predators. We provide some general observations on the behavior of the predators.

Chub mackerel attacked 6.7 mm larvae from a shorter distance than larger larvae (*t*-test, $P = 0.05$), but no statistically significant trend was evident when northern anchovy were predators. Mean attack distances were a poor measure of sighting range as they included repeated, short-range attacks on the larger larvae. We observed both predator species swimming within 2-3 dm of the smallest larvae without attacking them, whereas larger larvae were always attacked from this distance indicating that sighting distances may be shorter for small larvae.

Adult northern anchovy usually attacked a larva only once during a feeding sequence, and if the larva escaped, it was rarely attacked again or pursued. On the other hand, if the chub mackerel did not capture the larva on the first attack, it usually turned and attacked again. Chub mackerel usually chased an escaping larva until it was captured. The attack speeds of adult northern anchovy, although not measured, seemed to be similar over a wide range of larval prey sizes, whereas the attack speeds of chub mackerel clearly were faster when attacking larvae greater than about 10 mm SL than when attacking smaller larvae.

DISCUSSION

Factors Affecting Larval Vulnerability

A low level of responsiveness seems to be the dominant feature of the vulnerability of northern anchovy larvae to fish predators over the smallest larval size classes we tested (6-10 mm SL). Presumably northern anchovy larvae <6 mm would respond even less frequently, as Webb (1981) found that only 9% of 2.9 mm northern anchovy larvae responded to the aquarium fish *Amphiprion percula*, whereas about 30% of 6 mm larvae did so. During this period vulnerability of northern anchovy larvae to fish predators seems to be primarily a function of visual detection by the predator, because when the larvae are detected they have a low probability of escaping. Our data on predation rates and maximum attack distances indicate that predation in the sea on the small, young larval stages might be lower than expected because of the short range at which such larvae may be detected. Thus, factors that affect the distance at which larvae are detected by predators, such as larval size, visual contrast, and water clarity (Vinyard and O'Brien 1976), may be the most important variables during the first 3 wk of life. As larvae grow they more often respond to the attacks of predators and escape them more frequently. Maturation of visual and lateral line systems (O'Connell 1981) may be the principal cause of this general increase in responsiveness with larval length. Although older larvae are more responsive, they are also more readily detected by predators because they are larger and have more pigmentation. Improved avoidance behavior may not completely compensate for the greater visibility of larvae in the 8-12 mm range, as our data on predation rates by northern anchovy indicated that the rates of consumption were highest for larvae in this range.

Larvae longer than 20 mm responded more frequently to northern anchovy than to chub mackerel predators, possibly because chub mackerel attacked such large larvae at much higher speeds. At higher attack speeds, less time is available for the larvae to respond; consequently, predators with the most rapid attack speeds evoke the lowest proportion of prey responses (Webb 1982). Thus one might expect a larva to respond to small fish predators more frequently than to larger ones, since attack speed would be expected to increase with predator size. This may explain why northern anchovy larvae (2.9-12 mm SL) responded more frequently to the small *Amphiprion* (44 mm) (Webb 1981) than they did to either northern anchovy or chub mackerel predators (Fig. 4). The pectoral swimming of *Amphiprion* might also provide more cues of an impending attack than did the swimming movements of either northern anchovy or chub mackerel.

In addition to size-specific avoidance capabilities and visibility, many other larval characteristics affect their vulnerability to predators. We briefly consider here three of these: effects of starvation, effects of the onset of schooling, and effects of variations in larval growth rates. Clupeoid larvae undergo degradation of muscle and other tissues during starvation, and a reduced predator avoidance behavior might be anticipated (Ehrlich 1974; O'Connell 1980). In a preliminary experiment Folkvord (1985) reported that only 50% of starved, 33 mm northern anchovy larvae responded to the attacks of adult northern anchovy as compared with 100% for fed larvae. No starved 10 mm larvae escaped attack whereas 15-20% of the fed 10 mm larvae did so. The numbers of observations were insufficient for a statistical comparison, but recent work by Booman (unpubl. data, Southwest Fisheries Center, La Jolla, CA) indicates starvation can have a statistically significant effect on responsiveness of 10 mm northern anchovy larvae to adult northern anchovy predators.

The effect of the onset of larval schooling was not considered in these experiments; however, escape and response probabilities of individual larvae may not be altered greatly by the onset of schooling. The work of Major (1978) indicates that the most important effect of schooling may be to reduce the rate of attack by predators. He also found that the majority of Hawaiian anchovy captured by predators were isolated individuals that had moved away from the school, and predator success on schooled prey was similar to that on isolated prey. The onset of schooling in larval northern anchovy occurs between 11 and 15 mm SL, but the time spent in organized, cohesive schools increases throughout the northern anchovy's larval and juvenile periods (Hunter and Coyne 1982). Thus attack rates of predators might be expected to decline throughout later larval and juvenile life as the northern anchovy spends more time in cohesive schools. The onset of schooling occurs over the size range in which we observed the maximum predation rate (numbers consumed in 5 min) on individual northern anchovy larvae by northern anchovy predators. Thus predation pressure may be an important evolutionary factor in the timing of the onset of schooling during the larval stage.

The interaction between larval growth rate and size-specific vulnerability to predation may be an important source of interannual variation in larval mortality (Shepherd and Cushing 1980; Smith 1985). A simple calculation illustrates this point using the size-specific vulnerability of northern anchovy larvae (10-20 mm SL) to adult northern anchovy predators. We assumed larval escape ability to be an inverse measure of predator vulnerability and normalized it to the average mortality rate over this size interval (Table 1). Thus in our calculation, the rate larval mortality decreased with increasing larval size was inversely proportional to the rate escape ability increased with size (larval escape ability increased linearly with larval length over the 10-20 mm length range). Our calculation indicated that a 50% increase in growth rate from the average rate of growth in the sea resulted in a 58% increase in survival in 30 d compared with average conditions. Decreasing the growth rate by 50% gave a 37% decrease in survival over the same interval. A longer period of reduced or enhanced growth rates will, of course, give a larger deviation from average survival values.

TABLE 1.—Calculation of the effect of growth rate on survival of 10-20 mm northern anchovy larvae when mortality is inversely proportional to length specific escape probabilities.

Terms	Parameter values
Z = mortality rate	$Z = 0.05$ at 16 mm[a]
S = larval length (mm)	10 mm $< S <$ 20 mm
G = growth rate	$G = 0.325$ mm/d[b]
T = time	$T = 30$ d
N = relative numbers of larvae	$N(0) = 1$

Initial equations

$$Z = 0.15 - (0.00625 \times S)^{a}$$
$$S = 10 + (G \times T)$$
$$dN/dt = -(Z \times N)$$

Final equations after substitution and integration

$$N = 0.0724 \times \exp(2.808 \times G)$$

Estimates of survival after 30 days

Growing conditions	Growth rate (mm/d)	Relative numbers of larvae	Relative survival (%)
Average	0.325	0.1803	—
50% increase	0.488	0.2850	+58
50% decrease	0.162	0.1141	−37

[a] Mortality function generated from larval anchovy escape data with adult northern anchovy as predators. Values are normalized to Z 0.05 at 16 mm (Smith 1985).

[b] From Smith (1985), 0.325 ± 50% also used in calculation.

Effect of Predator Size

We examined the existing literature on predators of larval northern anchovies to determine how the ability to escape a predator varied among different predator species. Regardless of the predator species, larval escape ability always increases with larval size, but the rates vary greatly with predator size. In general the smaller the predator, the faster larval escape abilities improve with increasing larval length (Fig. 6). The results of our work on *E. mordax* were similar to those of Brownell (1985) on *E. capensis*. However, capture success of the 85 mm *E. mordax* predators used in our study was about 20% higher than the 34 mm *E. capensis* predators used by Brownell.

The extent of the predator field for a given size and species of predator can be defined as the larval size range in which larval escape success is <100%. For adult northern anchovy predators (85 mm and

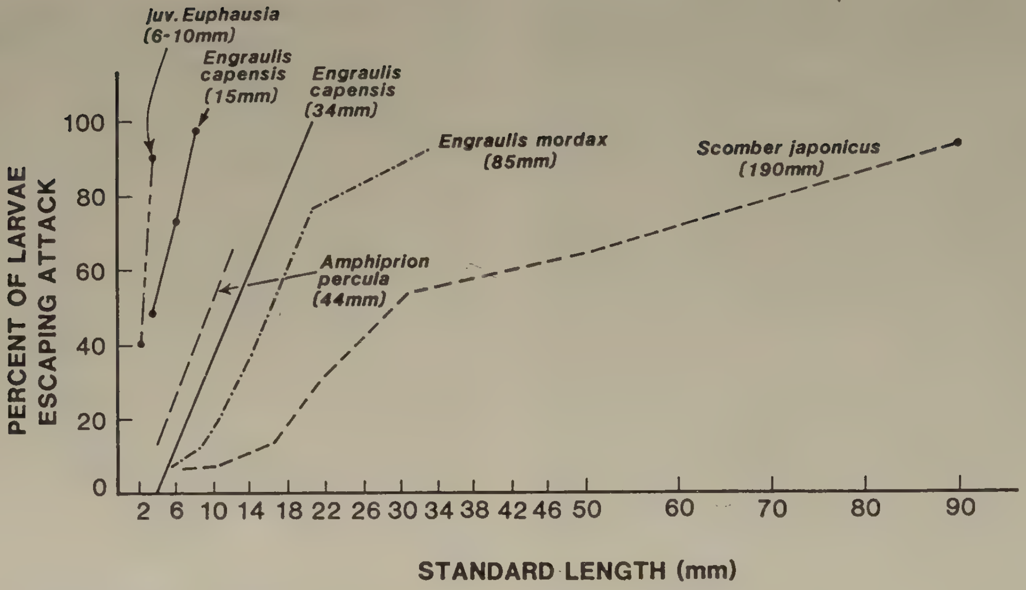

FIGURE 6.—Percentage of larval and juvenile anchovies escaping attacks of various predators as a function of length. Data for *Engraulis capensis* feeding on larval *E. capensis* are from Brownell (1984); juvenile *Euphausia* fed *E. mordax* from Theilacker and Lasker (1974); *Amphiprion percula* fed *E. mordax* from Webb (1981); and others are from this study. Numbers indicate length (mm) of the various predators.

larger), the field extends from the egg (Hunter and Kimbrell 1980) to about 40 mm. The field for juvenile chub mackerel is much wider than that for northern anchovy extending from northern anchovy eggs to adults (120 mm), whereas the predation field for *Euphausia* is restricted to the yolk-sac period (Theilacker and Lasker 1974). The limited data available (Table 2) provide a crude index for the upper limit of the predator field for northern anchovy larvae. When the larval length exceeds about 50% of the predator length little or no predation occurs.

TABLE 2.—Upper limit of some predator fields for larval anchovies, *Engraulis mordax* and *E. capensis*.

Predator		Upper limit of predator field[1]	
Species	Predator length (mm)	Larval length (mm)	Larval length / Predator length
Euphausia juveniles (Theilacker and Lasker 1974)	8	4.5	0.6
Engraulis capensis (Brownell 1984)	15	8.2	0.6
Engraulis capensis (Brownell 1984)	34	20	0.6
Amphiprion percula (Webb 1981)	44	18	0.4
Engraulis mordax (this study)	85	[2]∼40	0.5
Scomber japonicus (this study)	190	[2]∼120	0.6

[1] Upper limit = larval size at which all larvae escape predator.
[2] Extrapolated values.

CONCLUSIONS

Much of the past research on recruitment has focused on early larval stages where mortality rates are the highest (May 1974). Our work supports a growing contention that later larval stages and early juvenile stages may be as important in determining year-class strength (Smith 1985) and that such effects might be mediated through an interaction between larval growth and size-specific vulnerability to predators. Our results and those of others indicate that the ability of northern anchovy larvae to escape pelagic predators increases throughout the larval stage. On the other hand, the susceptibility of larvae to predation may not decrease strictly according to size because large larvae may be more easily detected by visual feeding planktivorous fishes than smaller ones.

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The Spawning of Skipjack Tuna from Southeastern Brazil as Determined from Histological Examination of Ovaries

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A total of 961 skipjack tuna ovaries from southeastern Brazil was examined to determine their reproductive condition. The Brazilian fish were sampled from November 1981 to July 1982 from the coastal area south of Cabo Frio between 22°S and 28°S latitude. A portion of the population was in near spawning condition in November and this condition continued through March. Ovaries obtained during May–July were mainly regressed. The smallest sexually mature female in our sample was 510 mm. The minimum gonad index of mature fish was 30. Histologically mature ovaries represent a wide range of gonad indexes, including ripening and recently spawned conditions.

Des ovaires de listaos du sud-est brésilien, au nombre de 961, ont été examinés afin d'en déterminer l'état du point de vue de la reproduction. Les poissons brésiliens avaient été échantillonnés entre novembre 1981 et juillet 1982 dans la zone côtière au sud du Cabo Frio, entre 22°S et 28°S de latitude. Une partie de la population s'y trouvait près de frayer, ce qui put être observé jusqu'au mois de mars. Les plupart des ovaires prélevés de mai à juillet étaient en phase de regression. La femelle mature de plus petite taille observée dans l'échantillon mesurait 510 mm. L'indice gonado-somatique minimum des poissons matures était 30. Les ovaires matures du point de vue histiologique représentaient une ample gamme d'indices gonadiques, dont les stades de maturation et d'après-ponte.

Se examinaron un total de 961 ovarios de listado de la costa Sudeste de Brasil para determinar sus condiciones reproductoras. Los peces brasileños fueron muestreados desde Noviembre 1981 a Julio 1982, en la zona costera al sur de Cabo Frio, entre los 22°S y 28°S de latitud. Una parte de la población se encontraba próxima al desove en Noviembre, y esta condición se mantuvo hasta el mes de Marzo. Los ovarios obtenidos durante Mayo–Julio estaban principalmente en fase regresiva. La hembra más pequeña sexualmente madura de la muestra, medía 510 mm. El índice mínimo de gónadas de peces maduros fue de 30. Ovarios histológicamente maduros representaron una amplia gama de indices de gónadas, incluyendo condiciones de madurez y puesta reciente.

1. Introduction

The skipjack tuna *Katsuwonus pelamis* is the most important pelagic resource in many areas throughout the tropical oceans, yet much remains to be learned about its biology, including its reproductive habits. Previous studies on maturation and spawning of skipjack have been conducted on populations from the following areas: Australia (Blackburn and Serventy 1981); western Pacific (Wade 1950; Asano and Tanaka 1971; Hu and Yang 1972; Naganuma 1979); central Pacific (Brock 1954; Marr 1948; Yoshida 1966); eastern Pacific (Schaefer and Orange 1956; Joseph 1963; Blackburn and Williams 1975); and Atlantic Ocean (Simmons 1969; Batts 1972c; Cayré 1981 and included references). The purpose of this paper is to provide information on skipjack reproduction from southeast Brazilian seas. The main objective of the study was to determine the season of spawning by means of histological examination of ovaries.

2. Methods

Gonads were obtained from skipjack taken off southeastern Brazil, south of Cabo Frio along the edge of the continental shelf between 22°S and 28°S (Figure 1). The fish were taken by live-bait boat and were initially frozen or iced.

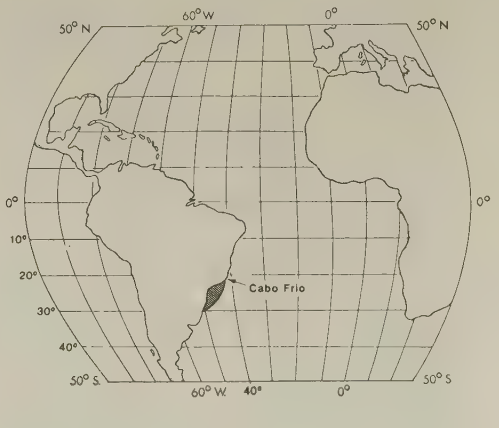

Figure 1. Fishing area (shaded) where Brazil samples were taken.

All gonad samples were fixed in 10% formalin. Some were later stored in isopropyl alcohol. Weights of fish and gonads were taken to the nearest 0.1 g; fork length measurements were taken to the nearest cm.

The ovary specimens were examined externally to determine if they were mature or maturing (enlarging). The smallest fish with mature ovaries in our sample was found to be 510 mm fork length.

A sample of 241 ovaries from fish larger than 510 mm was selected for histological examination of the spawning cycle. One section from the central axis of each ovary was used. Histological examination indicated that the fundamental ovarian structure was similar in all parts of the ovary. Yoshida (1966) similarly found this to be the case for Pacific skipjack.

Tissue was embedded in paraplast, and histological sections were cut at 8μm. Slides were stained with iron hematoxylin. Ovaries were then classified according to four stages of oocyte development: Regressed, Previtellogenic, Vitellogenic, and Mature (Table 1). Oocyte measurements were taken from the histological slides using an ocular micrometer.

Table 1. Histological classification of skipjack ovaries.

Stage	Condition of Ovary
1. Regressed Ovary	Primary oocytes (<100 μm diameter) predominate; mode at ca. 50 μm.
2. Previtellogenic Ovary	Vacuolated oocytes (100–300 μm diameter) predominate.
3. Vitellogenic Ovary	Oocytes with yolk deposition in progress (250–400 μm diameter).
4. Mature Ovary	Mature (yolk-filled) oocytes (400 + μm diameter) predominate. Yolk deposition typically progressing in smaller mode (250 μm) of vitellogenic oocytes. Postovulatory follicles may be present.

Because these ovaries had been subjected to freezing earlier in the sampling process, freeze damage was a possibility. We have noted in our results where cold related histological changes may have occurred. Such damage appeared to be minimal.

We did not examine the testes histologically. Histological studies of testes have proven less useful than those of ovaries for describing the spawning schedule of fish (Batts 1972c; Macer 1974).

For fecundity estimates, a small subsample (ca. 0.050 g) was taken from 24 ovaries which histological analysis had verified as being in spawning condition (containing a mode of yolk-filled oocytes). This subsample was weighed and all mature (yolk-filled) oocytes were counted under a dissecting microscope. These subsamples provided between 77 and 369 mature oocytes each. Total fecundity was then estimated by proportion. Relationships between total fecundity and body size, body weight, and ovary weight were determined by regression analysis.

Gonad indexes (G.I.) were calculated using the formula G.I. = $W/L^3 \times 10^8$, where W = weight in grams and L = length in mm, as used by other skipjack investigators (Schaefer and Orange 1956; Yoshida 1966; Batts 1972c). These measurements were taken from 581 fish. A larger sample of 1,905 fish was used to examine the sex ratio. Length frequencies of the fish whose ovaries were examined are shown in Figure 2. The ovaries of some of these fish were also examined histologically and the length-frequencies of these fish are also shown in Figure 2.

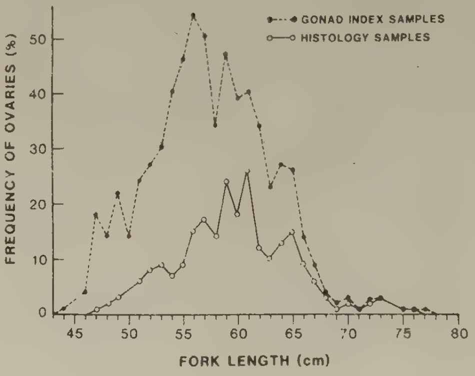

Figure 2. Length frequencies of Brazilian samples and the portions histologically examined.

3. Results

3.1 Histology

The ovaries of skipjack tuna are typical of other teleosts in consisting of paired, fusiform organs which are attached to each other at their posterior end by a mesentery. As skipjack can undergo a distinct seasonal spawning cycle, ovary size will vary depending upon the time of sampling. In the sample from Brazil, the ovaries comprised as little as 0.48% of total body weight when the fish were not spawning (July) or up to 4.02% of total body weight when the fish were in spawning condition (January). The ovary was composed of connective tissue septa which were lined with primary oocytes that averaged about 50 μm in diameter. This fundamental structural makeup was most evident when the fish were reproductively inactive, i.e. regressed (Stage 1, Figure 3A), as has previously been described by Batts (1972c). It was less evident when spawning was imminent.

The earliest histological sign of ovarian activity was the appearance of previtellogenic Stage 2 oocytes (Figure 3B). These oocytes were slightly enlarged, up to 300 μm diameter oocytes, and contained several rings of vacuoles situated along the inner periphery.

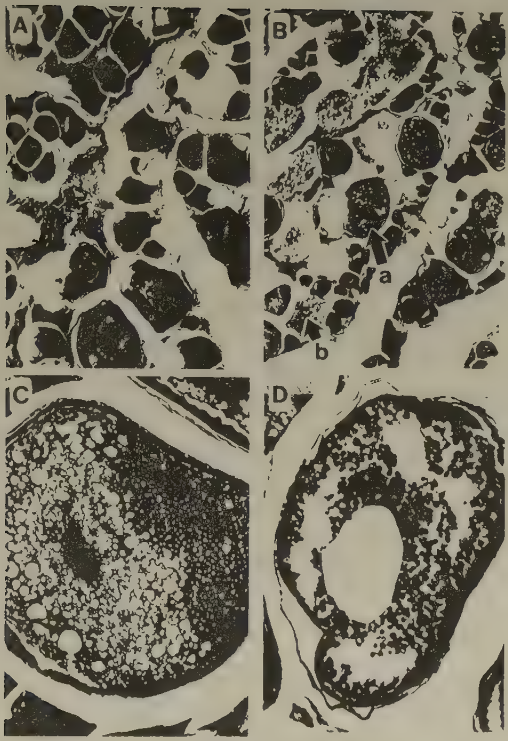

Figure 3. Photomicrographs of histological sections of skipjack ovaries from Brazil. (A) Primary oocytes from inactive ovary, 13 June; 111 X. (B) Secondary oocytes (arrow a), 2 February; atretic oocytes also present (arrow b); 69 X. (C) Vitellogenic oocyte containing dust-like yolk. Larger vacuoles may have contained oil prior to histological clearing; 15 January; 173 X. (D) Mature oocyte; note large vacuole; 15 January; 104 X.

The vacuoles presumably contained lipoidal substances that were removed by the histological clearing agent (xylene) during slide preparation. Previtellogenic oocytes became progressively more numerous in fish at a more advanced stage of the vitellogenic cycle, and eventually became the most abundant type present.

Vitellogenic oocytes with discernible yolk granules appear as the spawning cycle enters stage 3. These granules are very small (Figure 3C) and are "dust-like" in appearance. They clearly differ from the more usual, heavy yolk granules of other vitellogenic teleosts. The oocytes are up to about 400 μm in diameter. Similar appearing oocytes at this stage are shown by Cayré and Farrugio (this volume). However, this condition may be an artifact resulting from freezing of the tissue. Histological examination of freshly fixed, vitellogenic skipjack ovaries will be necessary to clarify this.

Finally, the mature ovary is characterized by the predominance of mature, yolk-filled oocytes of Stage 4. These averaged 498 ± 10.6 μm in diameter (= .50 mm) (n = 29, range 415–616 mm) prior to undergoing hydration which occurs just prior to spawning. Mature skipjack oocytes are similar to those of other teleosts in being surrounded by a granulosa layer and zona radiata. Some of the largest mature oocytes (Figure 3D) commonly contain large vacuoles in their centers. These may have contained oil prior to histological processing. In a few cases, postovulatory follicles were observed (Figure 4A). These showed some distortion from freezing but were otherwise similar in appearance to those seen in the northern anchovy *Engraulis mordax* by Hunter and Goldberg (1980). Also present were what appeared to be hydrated eggs which averaged 0.65 μm in length. These were distorted and may possibly have been mature oocytes that had become swollen and had ruptured during the freezing process. We did not observe running ripe ovaries, which would contain ova approximately 1.0 mm in diameter (Yoshida 1966).

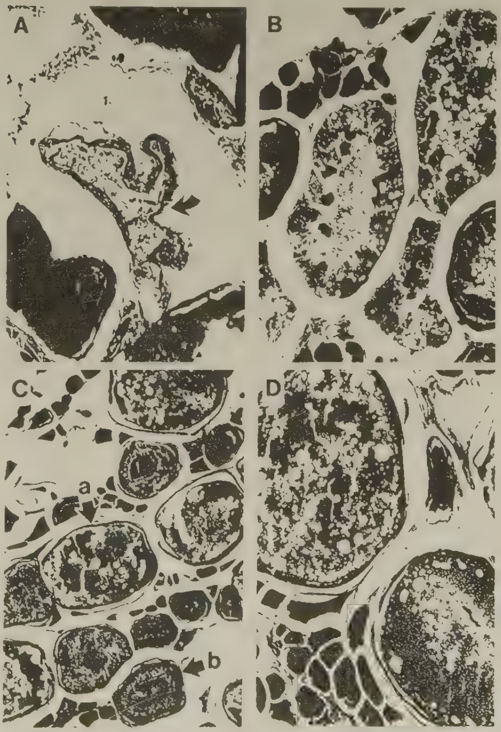

Figure 4. Photomicrographs of histological sections of skipjack ovaries from Brazil. (A) Post-ovulatory follicle (arrow) of uncertain age; some distortion from freezing; 276 X. (B) Atretic oocytes, 14 January; 173 X. (C) Mature (arrow a) and vitellogenic (arrow b) oocytes, 12 January; 173 X (D) Mature (upper left) and vitellogenic (lower right) oocytes, 12 January; 173 X

Atresia, or spontaneous degeneration of oocytes (Figure 4B), was observed frequently in fish of certain collections. For example, it was found in 11 of 18 skipjack examined from December 11, 1981. This condition, at the beginning of the spawning season, likely reflects environmental stress. High percentages of atretic oocytes are normally seen late in a spawning cycle, when oocytes that initiate but do not complete yolk deposition degenerate. Also, corpora atretica were commonly noted. These structures, which contain yellow brown granules, represent the last stage in the atretic process (Lambert 1970). Baglin (1982) observed them in the Atlantic bluefin tuna.

3.2 Seasonal Cycle

Histological examination of the ovaries indicated a spawning period from November through March, based upon the occurrence of mature ovaries (Table 2). It was not possible to positively designate when spawning began as no material was available form August to October. Nor were any running ripe ovaries ever seen. The number of spawnings per individual per season are not known, but the presence of a mode of mature oocytes (ripening and spawning imminent) and a vitellogenic mode for a subsequent spawning (Figures 4C, D) indicate that females spawn more than once per season. Brock (1954) and Bunag (1956) reported Pacific skipjack were multiple spawners, and Raju (1964b) claimed the same for Indian Ocean skipjack. Simmons (1969), Batts (1972c), and Cayré (1981) all reported multiple modes of ova diameters in Atlantic skipjack.

Table 2. Percentage monthly distribution of ovary maturity stages in Brazilian skipjack.[1]

Month	N	Stage: 1 Regressed %	2 Previtellogenic %	3 Vitellogenic %	4 Mature %
November 1981	6	16	0	16	67
December 1981	26	15	8	19	58
January 1982	44	4	7	16	73
February 1982	61	5	5	28	62
March 1982	31	10	10	35	42
April 1982	15	60	6	27	6
May 1982	28	89	8	3	0
June 1982	16	100	0	0	0
July 1982	14	100	0	0	0

[1] These were mature sized fish, greater than 510 mm FL.

The frequency of the four histological stages varied according to fish size (Figure 5). The majority of fish fell within the 550–650 mm size class, and most spawning activity probably occurred during December–February, when histological stage 4 predominated. Notice that during this season, larger fish tending to have a high proportion of individuals with mature ovaries entered the sample.

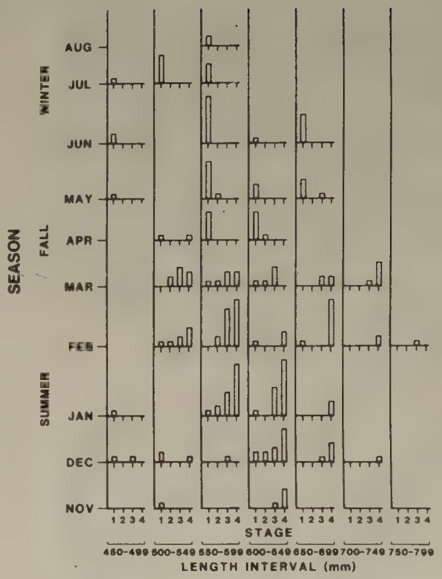

Figure 5. Frequency of occurrence of four histological stages of skipjack ovaries from Brazil, by month and by fork-length interval.

The gonad indexes reflected the same spawning seasonality. They were increased greatly in November–March and then reduced in April–July (Table 3, Figure 6). Some immature fish with small gonad indexes were found in all months, so that monthly distributions of values were highly skewed. The mean index values, which should be normally distributed, are shown with normal 95% confidence intervals.

Table 3. Summary of length, weight, gonad weight, and gonad index data with standard errors for Brazilian skipjack.

Month	N	Body Length (mm) $\bar{x}$	$S_{\bar{x}}$	Body Weight (g) $\bar{x}$	$S_{\bar{x}}$	Gonad Weight (g) $\bar{x}$	$S_{\bar{x}}$	Gonad Index $\bar{x}$	$S_{\bar{x}}$
Nov. 1981	17	610.0	9.0	5229.4	242.9	66.0	7.2	28.0	2.7
Dec. 1981	56	589.4	6.4	4828.6	189.3	72.2	6.9	32.4	2.3
Jan. 1982	87	591.4	3.8	4380.5	103.5	78.0	5.2	35.0	2.0
Feb. 1982	75	600.3	5.9	4565.3	148.1	113.9	6.3	49.1	2.2
March 1982	78	581.9	7.8	4380.8	201.6	66.2	6.0	30.9	2.4
April 1982	86	578.9	3.5	4438.4	85.6	28.3	2.1	14.5	1.0
May 1982	91	600.5	4.5	4949.4	55.7	26.9	1.1	12.2	0.3
June 1982	45	596.1	5.7	4382.2	129.4	21.8	0.9	10.1	0.3
July 1982	46	554.3	4.6	3204.3	111.9	15.7	0.7	9.1	0.3

3.3 Gonad Index and Fork Length at Maturity

There were 94 fish with mature, histological stage 4 ovaries. For these fish, spawning would soon occur or had already occurred. Their average gonad index was 56.70 ± 3.0. Most had indexes between 40 and 80 (Figure 7). Our minimum gonad index recorded for a sexually mature skipjack was 31, from a 620

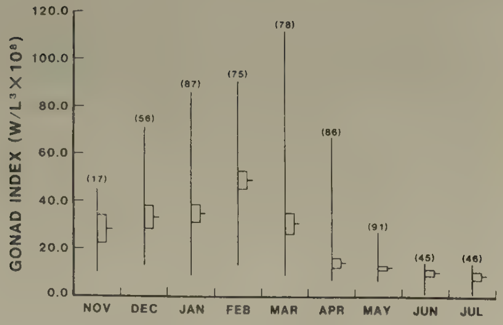

Figure 6. Seasonal gonad indexes for Brazilian skipjack. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval of mean. Sample size above each month.

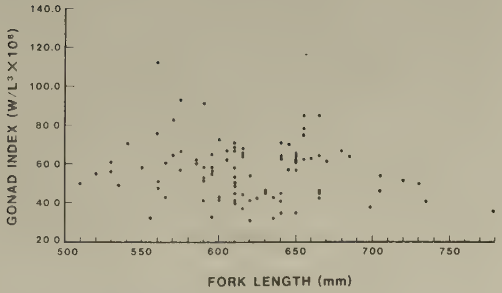

Figure 7. Relationship between gonad index and fish size for mature Brazilian skipjack.

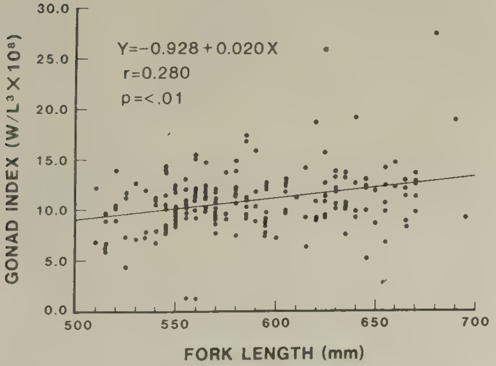

Figure 8. Relationship between gonad index and fish size for reproductively inactive Brazilian skipjack, May–July 1982.

mm fish which contained a mode of yolk filled oocytes. During May–July, when the Brazilian population was reproductively inactive, most indexes fell between 5.0 and 15.0 (Figure 8). Orange (1961) similarly found that only skipjack with indexes over 30 approached maturity.

Yoshida (1966) found that the mean diameter of the most mature mode of oocytes changed little between gonad indexes 35 and 96, and approached an asymptote of about 0.6 mm. Batts (1972c) suggested that gonad indexes for skipjack may exceed 100, and Naganuma (1979) found that skipjack with mature oocytes had indexes of 80 or higher. Evidently skipjack with mature ovaries can obtain a wide range of index values over 30. Furthermore, there is a tendency for gonad indexes to increase with size of fish (Orange 1961). That the relationship of ovary to fish weight may not be linear with increasing fish weight for fish of the same histological stage (i.e. ova diameter) was shown by Hunter and Goldberg (1980) for *Engraulis mordax*.

Our smallest mature or maturing skipjack was 510 mm. There were two such fish. One was vitellogenic (stage 3) with gonad index 45.5; the other was mature (stage 4) with gonad index 50.8. This size is within the range given by Orange (1961), who found that eastern Pacific skipjack from the Revilla Gigedo Islands matured at 550 mm, while those from Cocos Island matured at 400 mm. Miminum size at sexual maturity of skipjack in the Atlantic, Pacific, and Indian Oceans has typically been reported between 400 and 450 mm (Marr 1948; Wade 1950; Brock 1954; Yabe 1954; Postel 1955; Bunag 1956; Schaefer and Orange 1956; Orange 1961; Ronquillo 1963; Raju 1964a; Yoshida 1966; Simmons 1969; Hu and Yang 1972). Chur et al. (1980) reported that skipjack mature in the eastern tropical Atlantic at 390 mm, while Batts (1972c) reported an average of 500 mm for North Carolina fish. Cayré and Farrugio (this volume) determined that 420 mm was the length at which 50% of eastern Atlantic skipjack attain a gonad index of 35 or more. The difference in their value of 420 mm and ours of 510 mm for Brazilian skipjack is due in part to their sampling only from schools in which 50% or more of the females were sexually mature. Furthermore, fish caught off Brazil are larger than those caught in the eastern Atlantic (c.f. Cayré et Farrugio this volume), our smallest specimen being 440 mm.

3.4 Fecundity

Our fecundity estimates, based on counts of mature oocytes, varied between 129,807 and 977,566 eggs. The fish were between 510 and 720 mm in length (Table 4). Average fecundity was 385,937 eggs. Values from other skipjack studies are given in Table 5. Our values fall within the range reported in these other investigations, but averaged lower. They are similar to the estimate from the eastern Atlantic of 100,000 to 1,000,000 eggs (Cayré et Farrugio, this volume). Matsumoto et al. (1984) noted the difficulty of the problem of estimating annual egg production, in part because of the large variability among individuals, even of the same size, and because of the uncertainty of the number of multiple spawnings. The oocytes we counted appeared to be from a discrete

Table 4. Length, weight, and fecundity data and regressions for 24 Brazilian skipjack females

	Body Length (mm) X_1	Body Weight (g) X_2	Gonad Weight (g) X_3	Fecundity Estimate Y
	720	8000	195.3	334263
	705	7300	191.5	627868
	680	7000	210.9	421800
	660	6000	183.3	456583
	655	5700	211.3	516930
	650	6000	172.2	977566
	620	4800	129.8	302080
	615	4700	155.2	411460
	615	5100	150.6	374963
	615	4900	158.7	275479
	610	4500	148.0	443816
	610	4600	135.0	259411
	605	4200	167.4	340200
	595	4300	123.2	588000
	580	4100	114.6	326731
	580	4000	104.9	270642
	580	3800	104.6	157925
	575	3700	109.2	429354
	575	3900	148.2	406327
	575	3500	126.0	271551
	570	3700	118.6	492447
	550	3000	96.5	250245
	520	2600	77.3	197039
	510	3000	67.4	129807
$\bar{x}$	607.08	4683.33	141.65	385936.96
$S_{\bar{x}}$	10.60	282.05	8.13	36419.49

Fecundity Regressions:

$Y = 681760.759 + 1758.733\,X_1 \qquad r^2 = .262$

$Y = 87698.857 + 63.681\,X_2 \qquad r^2 = .243$

$Y = 47265.033 + 2390.863\,X_3 \qquad r^2 = .285$

Table 5. Fecundity estimates of skipjack from previous studies

Area	Size range (mm)	Estimate	Worker
Brazil	510–720	129807– 977566	This study
N. Carolina, USA	498–704	141000–1200000	Batts (1972c)
Tropical Atlantic	465–809	262000–1331000	Simmons (1969)
Eastern Pacific	640–710	480000–1000000	Schaefer (1962)
Hawaii	440–870	280000–1900000	Rothschild (1963)
Japan	468–610	110000– 860000	Yabe (1954)
Minicoy, Arabian Sea	418–703	151900–1977900	Raju (1963, 1964b)
Marquesas Islands Pacific Central	430–740	100000–2000000	Yoshida (1966)
Eastern Pacific	614–715	400000–1330000	Joseph (1963)

mode; however, errors are possible if the size modes intergrade or if development is gradual within modes (Hunter and Goldberg 1980).

The relationships between number of mature oocytes and fish length, fish weight, and ovary weight were calculated using linear regression and are given in Table 4. All regressions were positive and significant ($P < .05$). The regression between fecundity and fish length was most similar to that of Batts (1972c) but predicted a lesser fecundity by about 21% for 600 mm fish. Because of the small sample size and the problem of the meaning of ova counts with respect to total fecundity, these relationships should be considered tentative.

3.5 Sex Ratio

The sex ratio in the sample from Brazil was examined, and additionally, a second Brazilian sample (Brazil-2) was examined. The Brazil-2 sample originated from the same fishery as did our primary Brazilian sample, but was sampled in Puerto Rico after transshipment from Brazil. The 1,358 skipjack of our primary Brazilian sample did not depart significantly from a 50:50 ratio of males to females, but the Brazil 2 sample did (Table 6). On five sampling dates of the latter, there were significantly more females than males collected. However, the heterogeneity χ^2 of the Brazil 2 sample was also highly significant, indicating heterogeneity of ratios among the constituent samples taken on different days. The heterogeneity χ^2 of the primary Brazilian sample was not significant, although its probability level was only 9%.

Table 6. Skipjack sex ratios and Chi-square tests.

Sample	N	Males	Fe-males	Tests of Departure from 1:1	d.f.	χ^2	P
Brazil (primary sample)	1358	703	655	Sum, 28 samples	28	39.27	>.05
				Pooled	1	1.70	>.05
				Heterogeneity	27	37.57	>.05
Brazil-2	547	241	306	Sum, 27 samples	27	67.00	<.01
				Pooled	1	7.72	<.01
				Heterogeneity	26	59.28	<.01

Cayré and Farrugio (this volume) examined the sex ratio from a larger Brazilian sample of 2,743 fish (of which our specimens were a subsample). They reported a male:female ratio of 1.10, a significant departure from sexual parity. However, their even larger Atlantic-wide sample showed no such departure. Evidently the deviation from a 50:50 sex ratio in the Brazilian samples increased faster than did the effect of sample size, leading to a statistical change in ratio, where heterogeneity was not balanced out in the pooled sample. We therefore, do not find sufficient reason to reject the hypothesis of a 50:50 sex ratio in the Brazilian skipjack.

4. Discussion

In Table 7 we compare the morphological gonad stages of Batts (1972c) with the corresponding histological stages of this study. In the same table are listed the average gonad indexes corresponding to our histological stages. The average difference in index between vitellogenic and mature ovaries was smaller than the difference between the previtellogenic and vitellogenic stages. This is not unexpected as there was only a slight size increase from vitellogenic oocytes (diameter 0.30–0.40 mm) to mature oocytes (0.50 mm). Notice that our histological mature stage includes Batt's late maturing, ripe, and spawned stages. Though we did not see ovaries that were clearly ripe (i.e. containing a mode of enlarged oocytes up to ca. 1.0 mm in diameter) or ovaries clearly spawned out (i.e. ovaries flabby and regressing), our histological mature stage did contain some postovulatory and atretic follicles. These ovaries were apparently ready to spawn and in some cases this must have already occurred to a limited extent.

Table 7. Comparison of skipjack morphological stages (Batts, 1972) with mean gonad index values (with standard errors of means) and histological stages from this study

Morphological Stage Batts (1972)	Average Gonad Index (this paper) N	$\bar{x}$	S_x	Histological Stage (this paper)
Stage 1: Immature	181	10.9	0.2	Stage 1: Regressed
Stage 2: Early maturing	9	25.5	2.8	Stage 2: Previtellogenic
Stage 3: Late maturing	32	46.2	2.8	Stage 3: Vitellogenic
Stage 3: Late maturing	94	56.7	1.5	Stage 4: Mature
Stage 4: Ripe	Not directly observed			Stage 4: Mature, but with mode of ripe ova ca. 1.0 mm in diameter.
Stage 5: Spawned	"		"	Stage 4: Mature, but with abundant postovulatory follicles.

Our size for mature oocytes averaged 0.50 mm in diameter and were smaller than the maximum sizes recorded for ripe skipjack ova by Batts (1972c), Yoshida (1966) and Kaya et al. (1982). They worked with fresh material and it is conceivable that some shrinkage occurred in the freezing process of our material. Yoshida (1966) described an advanced stage of oocyte development with well developed oil globules; this class had a mean diameter of 0.49 to 0.74 mm. The mature oocytes we describe could correspond to the lower size limit of this group. Yoshida's description of ova from a running-ripe fish included a mean diameter of 0.96 mm. This likely corresponds to the "ripe fish" described by Batts (1972c). That our collections did not contain fish with running-ripe ovaries is likely the main reason why our maximum ova sizes were smaller.

Running-ripe skipjack are apparently rare in collections. We believe this is because batch spawning (Hunter and Goldberg 1980) occurs and is completed rapidly. Yoshida's (1966) study also suggests that the transition of oocytes to the ripe condition with diameters greater than 0.65 mm is not gradual. Because hydration of ova and subsequent spawning may be rapid, even the hour of sampling can change the gonad stages that are observed (DeMartini and Fountain 1981). Recently Kaya et al. (1982) showed that captured and confined skipjack would ovulate within 8 hours after capture as a response to the stress. These fish were apparently in the unovulated stage at capture, with oocytes of the largest modal size no larger than 0.74 mm average diameter.

As in our study, Cayré and Farrugio (this volume) found very few oocytes larger than 0.50 mm in diameter among mature skipjack from the eastern Atlantic. Since their specimens included mature and post spawned ovaries, this also suggests that batch spawning is a transitory phenomenon.

Table 8 summarizes spawning times reported from different areas of the world's tropical seas. It might at first appear that skipjack are predominantly summer spawners. However, there are reports of year-round spawning, bimodal spawning (two periods of spawning in one year), and one report of winter–spring spawning. Considering the sampling problems, it is likely that skipjack are year-round spawners in the tropics and spring–fall spawners in the subtropics (Matsumoto et al. 1984). The Brazilian area has a subtropical oceanographic climate with seasonal and other periods of upwelling (Mascarenhias et al. 1971). Our data indicate spawning occurs during the southern summer off eastern Brazil, and in this regard is in keeping with the summer spawning times in the majority of previous studies from similar areas. However, inter-year variations in spawning pattern and size classes present can affect the perceived spawning season. Length of spawning season varies with fish size within a given population and larger fish probably travel and spawn over a wider area than do smaller fish. In the eastern Pacific, skipjack from California to Chile appear typically to migrate to the central Pacific to spawn (Orange 1961; Klawe 1963; Rothschild 1965).

The presence of larvae also provides evidence for the spawning season. Matsuura (1982a) reported that on two cruises along the eastern Brazilian coast (June and November–December), skipjack larvae were more abundant in the November–December (spring) cruise. Kikawa and Nishiwaka (1979) summarized plankton samples collected between 1959 and 1971 and reported skipjack larvae occurring off this same coast during both January–March and October–December. These results are consistent with our study which shows the presence of ready-to-spawn skipjack in collections from these same seasons from the nearby area south of Cabo Frio, Brazil.

Table 8. Summary of spawning times for skipjack from different regions.

Area	Spawning Time	Worker
Spring–summer spawners		
Brazil	November - April (southern hemisphere)	This paper
N. Carolina, USA	Late June–early July	Batts (1972c)
Cuba	May, June, July	Suarez-Caabro and Duarte Bello (1961); Gorbunova and Salabarria (1967)
Florida	April - May, July - August	Klawe (1960)
Marshall Islands	July August	Marr (1948)
Cape Verde Islands	May - September	Postel (1955)
Hawaii	February or April, - September	Brock (1954)
Marquesas and Tuamotu Islands	November April (southern hemisphere)	Yoshida (1966)
Senegal	May- September	Frade et Postel (1955)
Southwest Pacific 0° = 24°S	October March	Argue et al. (1983), Naganuma (1979)
Year-round Spawners		
Eastern, Western, Tropical Atlantic Ocean	Year-round	Simmons (1969)
Cuba	Year-round	Howell-Rivero y Juarez Fernandez (1954)
Bi-modal Spawners		
Western Pacific	August September, December–January	Asano and Tanaka (1971)
Indian Ocean	January - April, June–September	Raju (1946a)
Winter–spring Spawners		
Costa Rica	March - April	Schafer and Marr (1948)

The reproductive behavior of skipjack is likely complex. Cayré (1981) reported that skipjack from off Dakar, Sénégal did not appear to have a well-defined spawning period and suggested that the schedule of sexual maturation and spawning could be different for each school, depending upon the conditions that the school had been encountering. Off southern Brazil spawning regimes may be equally complex because of upwelling, the passage of weather fronts, and the interaction of the Brazil Current with the coastal shelf.

Since mature ovaries include a wide range of gonad index values, the index is not a precise indication of maturity stage. Matsumoto et al. (1984) concluded that gonad indexes were not good measures of skipjack maturity (i.e. ova size). However, gonad indexes above 30 do indicate ovaries that are ready for spawning with ripening soon to follow. Our observations of histological stage 4 ovaries with postovulatory follicles present indicate that this stage also includes some fish that had already batch-spawned.

The large variance of the gonad index for maturing and mature ovaries may be due to the following: (1) Ova do not ripen gradually, and the separating mode of ripening eggs (ca. 0.5–1.0 mm) may include a relatively large percentage of the total ova. Alekseyev and Alekseyeva (1981) considered this to be a feature of neritic tunas. (2) Ripening fish probably become increasingly unavailable to the fishery, as indicated by their rareness in samples (Brock 1954; Yoshida 1966; Batts 1972c; Chur et al. 1980). (3) Individuals from the same school tend to be at similar developmental stage, independent of other schools (Yoshida 1966; Cayré 1981) indicating a wide range of origins, ages and conditions of fish in a given area. (4) The physical condition of fish may change rapidly during the ripening, spawning, and post spawning stages.

The above factors do not necessarily indicate that spawning is erratic in time, depending upon the recent histories of individual schools. Rather, in a given spawning area total spawning may be almost continuous, due to the summation of individual spawning activity of numerous, independent schools. Therefore, total egg production may be much less variable than suggested by the observed variance of gonad index.

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The physiology of digestion in fish larvae

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Synopsis

The acquisition, digestion, and assimilation of food is critical for the growth and survival of fish larvae; a fish larva either grows or it perishes. Fish larvae are characterized by digestive systems and diets that differ from adults. Larvae undergo a pattern of trophic ontogeny, changing diet with increasing size, and these changes result in differences in digestive requirements. At first feeding, the larval alimentary canal is functional, but is structurally and functionally less complex than that of adults. The larval alimentary canal remains unchanged histologically during the larval period before transformation. During transformation, major changes that result in the development of the adult alimentary canal occur. The ontogeny of the alimentary canal differs in different taxa, and experimental evidence suggests that functional differences exist as well. Assimilation efficiency may be lower in larvae than it is in adult fishes, due to a lack of a morphological and functional stomach in larvae, but the question of improving assimilation efficiencies during larval development before transformation remains unresolved.

Introduction

The alimentary canal of fish larvae is morphologically, histologically, and physiologically less elaborate than the alimentary canal of adult fishes. Unlike the gradual development of some other organ systems, e.g., the integumentary, visual, musculature, and acoustic-lateralis systems (see review in O'Connell 1981), the development of the alimentary canal from the simple, undifferentiated, straight incipient gut of the yolk-sac larva to the complex, segmented alimentary canal of the adult proceeds by periodically rapid changes rather than continuous gradation. The incipient gut remains unchanged during yolk and oil-globule absorption (several days or weeks), then changes rapidly just before first feeding (1 to 3 d). In the main, the larval alimentary canal remains unchanged during the long larval period (several months to a year), then changes rapidly into the adult alimentary canal during transformation of the larval to the juvenile fish (weeks or months). [We use the terminology of Kendall et al. (1984) in describing early life history stages].

Concomitant with growth and the changing complexity of the alimentary canal are marked differences in diets. Most fish larvae are visual, raptorial planktivores (Hunter 1981) regardless, of whether their adult counterparts are indiscriminant filter-feeders, pelagic carnivores, or benthic pickers. Larvae begin feeding on large phyto- and small zooplankters and follow by feeding on increasingly larger zooplankters (Hunter 1981). For some species,changes in diets are required. For example, northern anchovy, *Engraulis mordax*, larvae survive on the dinoflagellate *Gymnodinium splendens*, but do not grow well beyond 6 mm in length unless larger food organisms are included in their diets (Hunter 1977). The diets of fish larvae change again during transformation.

The alimentary canal of fish larvae also shows considerable diversity among taxa and several general dichotomies are valid. The alimentary canal of precocial larvae that generally hatch from large, negatively buoyant eggs, is more developmentally advanced than the canal of altricial larvae that hatch from small, positively buoyant eggs (terminology from Balon 1979, 1981). The larvae of most 'lower' fishes (e.g., clupeoids, salmonids, and cyprinoids) have a straight alimentary canal, whereas the larvae of 'higher' fishes (e.g., paracanthopterygians and percomorphs have a looped canal). Notable exceptions to the latter generality are some ostariophysans and salmonids that have looped guts (Iwai 1969) and some stomiatoids that have unusual, trailing, exterilial guts (Moser 1981). Other peculiarities include the occluded guts of elopomorph leptocephali (Hulet 1978, Smith 1984).

The varied structural adaptations of the fish larvae alimentary canal and the changes of these adaptations with development are characteristic of differing functional adaptations to diets and prey concentrations. There is some evidence that ingestion and digestion rates as well as assimilation efficiencies are adapted to maximize larval growth and that these adaptations differ among taxa (Houde & Schekter 1980, 1983). Within taxa, digestion rates and assimilation efficiencies may change with prey availability and ration size (Werner & Blaxter 1980, Boehlert & Yoklavich 1984a) as well as with development (Laurence 1977, Buckley & Dillmann 1982). Here we consider the morphological and histological development of the alimentary canal, review histochemical and enzymological assays of larval alimentary canal function, and describe physiological studies of larval digestion and assimilation. While this paper is a review, we also include original observations and offer recommendations for future research.

Methods

Morphology and histology

Standard histological techniques, light microscopy, transmission electron microscopy (TEM), and scanning electron microscopy (SEM), have contributed to the understanding of the structure and function of the alimentary canal of fish larvae. Standard paraffin procedures have been used with some success for light microscopy (O'Connell 1981), but techniques that use glycol methacrylate as an embedding medium (Govoni 1984) are preferred. Procedures used for TEM of larval tissues are standard (e.g., see Iwai 1969). Boehlert (1984) offers techniques for the preparation of soft larval tissues for examination with SEM.

Histochemistry

The use of horseradish peroxidase (HRP) as a histochemical tracer has resolved the morphological sites and cytological mechanisms of protein absorption in fish larvae (Stroband et al. 1979, Stroband & Kroon 1981, Watanabe 1981, 1982a, 1984a). An advantage of the HRP technique is that in addition to allowing the observation of protein absorption, the technique affords an assessment of enzymatic hydrolysis. For the present observations, 0.5% HRP solution in physiological saline was injected into the larval alimentary canal through a glass capillary inserted into either the foregut or anus. The injection volume was adjusted to fill the entire lumen. Following incubation in vivo, tissues were fixed for 4 h in cold 5% glutaraldehyde in 0.1 molar phosphate buffer (pH 7.6) and then were washed at least overnight in the same cold buffer containing 5% sucrose. For light microscope observations, the tissues were frozen and cut into 10 μm thick sections. The sections were mounted on glass slides and incubated for 5–15 min at room temperature in 0.05% 3,3-diaminobenzidine tetrahydrochloride (DAB) in 0.05 M tris-HCl buffer (pH 7.6) containing 0.01% H_2O_2 as a substrate of HRP. They then were washed in 70% alcohol and observed. Peroxidase activity was detected with light microscopy as dark brown deposits. For TEM, the tissues were cut into small pieces, incubated in DAB, washed in distilled water, and postfixed for an hour in cold 1% OsO_4 solution in phosphate buffer (pH 7.3) containing 0.54% sucrose. This was followed by standard TEM preparations, but sections were observed without staining; peroxidase activity can be detected as electron-opaque deposits. Controls for both light and TEM were designed to show that there was no reaction product when either HRP or its substrate was absent. Groups of larvae or tissues were administered only physiological saline and observed, while another group was administered HRP solution, but without H_2O_2 substrate.

Ikeda (1959) and Prakash (1961) examined the histochemistry of alkaline phosphatase in the alimentary canal of fish larvae. Both used standard paraffin histochemical methods, although improved techniques with glycol methacrylate sections are now developed (Higuchi et al. 1979).

Enzymology

The digestive enzymes of fish larvae have been studied by testing enzyme activities of tissue homogenates against dissolved substrates (Tanaka et al. 1972, Kawai & Ikeda 1973a, 1973b, Dąbrowski 1982), whereby reaction products or the disappearance of substrates are measured photometrically; by testing the enzyme activities of tissue sections against substrate films, whereby the disappearance of substrate is assessed with light microscopy after histochemical staining (Szlaminska 1980, Vu 1983); and, by radio-immunoassay (Hjelmeland et al. 1983). The activities of amylase, maltase, pepsin, trypsin, chymotrypsin, and aminopeptidase have been assayed with the tissue homogenate method; the activities of amylase, pepsin, trypsin and chymotrypsin, and lipase with the substrate-film method. Trypsin and trypsinogen have been radio-immunoassayed.

Peristalsis and digestion rates

Peristalsis and evacuation rates of the alimentary canal have been studied by gross observation of live larvae (Blaxter & Hempel 1961, Chitty 1981, Pedersen 1984) and by collecting feces after larvae were fed. Enhanced resolution of evacuation rates can be obtained by feeding larvae alternately with stained and unstained food organisms (Laurence 1971) or with radioactively labeled food and unlabeled food. The latter technique also affords continuous as well as pulsed feeding experiments.

Assimilation

The use of the physiological energetic approach (Brett & Groves 1979) and of radiotracer techniques (Sorokin 1966) have provided assessments of assimilation efficiency of the larval alimentary canal. Assimilation is normally a difficult physiological parameter to measure (Johannes & Satomi 1967, Conover 1978). This problem is particularly difficult for fish larvae because of their small size, planktonic habitat, and lack of discrete feces production. The alimentary canal of fish larvae discharges both liquid and solid feces, and it is often impossible to separate excreted products of catabolism from defecated dissolved feces. As a result, assimilation efficiency is often estimated by difference, i.e., by the subtraction of other measurable energetic parameters from the matter or energy of ingested food. Assimilation efficiency as calculated by the differences in energy budget parameters is subject to the cumulative biases of these measurable parameters. Radiotracer methods offer a direct, short-term measure of assimilation, but are also subject to error. Based on the retention of metabolically active tracers (e.g., ^{14}C, ^{3}H, or ^{32}P), estimates of assimilation can be biased if the specific activity of the tracer in the food changes during the experiment, or if there are metabolic pools of unknown boundaries and rapid turnover rates that result in short-term loss of tracer from the animal (Conover & Francis 1973). Applications of radiotracer methods to fish larvae are discussed in Govoni et al. (1982) and Boehlert & Yoklavich (1984a).

Results and discussion

The development of the alimentary canal

The development of the alimentary canal of fishes encompasses morphological, histological, and functional changes that are aligned with major changes in gross morphology (Fig. 1). Here we describe the development of the alimentary canal of a generalized altricial larva with exceptions noted where marked variations occur. Embryonically, the alimentary canal develops from the involution of columnar endodermal cells that lie above the yolk (Devillers 1961). At hatching, the alimentary canal is a straight tube lying dorsal to the yolksac, is closed at the mouth and anus in some species, and is histologically undifferentiated along its length (Engen 1968, Tanaka 1969a, Fukusho 1972, Umeda & Ochiai 1973, Vu 1976, Govoni 1980, O'Connell 1981). The incipient gut remains unchanged until the completion of yolk- and oil-globule absorption when the undifferentiated tube becomes segmented by muscular valves into a buccopharynx, fore-, mid-, and hindgut (Kostomarova 1962, Engen 1968, Tanaka 1969a, 1969b, Fukusho 1972, Umeda & Ochiai 1973, Govoni 1980, O'Connell 1981). With the exception of some precocial young that develop from negatively buoyant eggs, most notably the salmonids, gasterosteids, and mouth brooding cichlids, fish larvae lack both a morphological and functional (secretory) stomach; the posterior region of the foregut (Watanabe & Sawada 1985) and the midgut (Govoni 1980) can expand and function to store food in some larvae. The larval alimentary canal remains largely unchanged until the onset of transformation. The development of a stomach and pyloric caeca from the posterior foregut accompanies transformation and constitutes the last major morphological change of the alimentary canal. The liver and pancreas (along with their ducts) are formed at hatching and are functional by the end of yolk absorption (Tanaka 1969a, 1969b, Vu 1976, Govoni 1980, O'Connell 1981, Watanabe & Sawada 1985).

An interesting exception to the above pattern of early gut development occurs in rockfish, *Sebastes*, embryos. This group is characterized by small eggs and high fecundity and has typically been referred to as being a primitive ovoviviparous genus (Wourms & Cohen 1975). Boehlert & Yoklavich (1984b), however, demonstrated that embryos receive additional nutrition during gestation. The uptake of nutritional substances by *S. melanops* embryos does not occur across epidermal surfaces, as in many other viviparous species (Veith 1980). Epidermal microridges on *Sebastes* embryos, characteristic of fish larvae epidermis (Yamada 1968, Roberts et al. 1973), are present, but microvilli, characteristic of epidermal absorptive surfaces on embryos of viviparous fishes (Veith 1980), are absent (Fig. 2a). Instead, uptake occurs across the alimentary canal mucosa, which develops while the embryo is still within the egg envelope and a significant yolk mass remains (Boehlert & Yoklavich 1984b). Histological observations on the alimentary canal of *S. melanops* embryos demonstrate that in early embryos the foregut is not open,

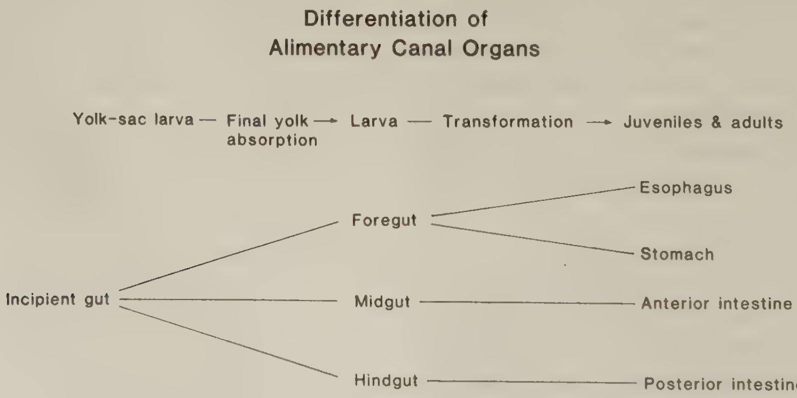

Fig. 1. The derivation, sequence, and timing of alimentary canal organs in typical larval fishes.

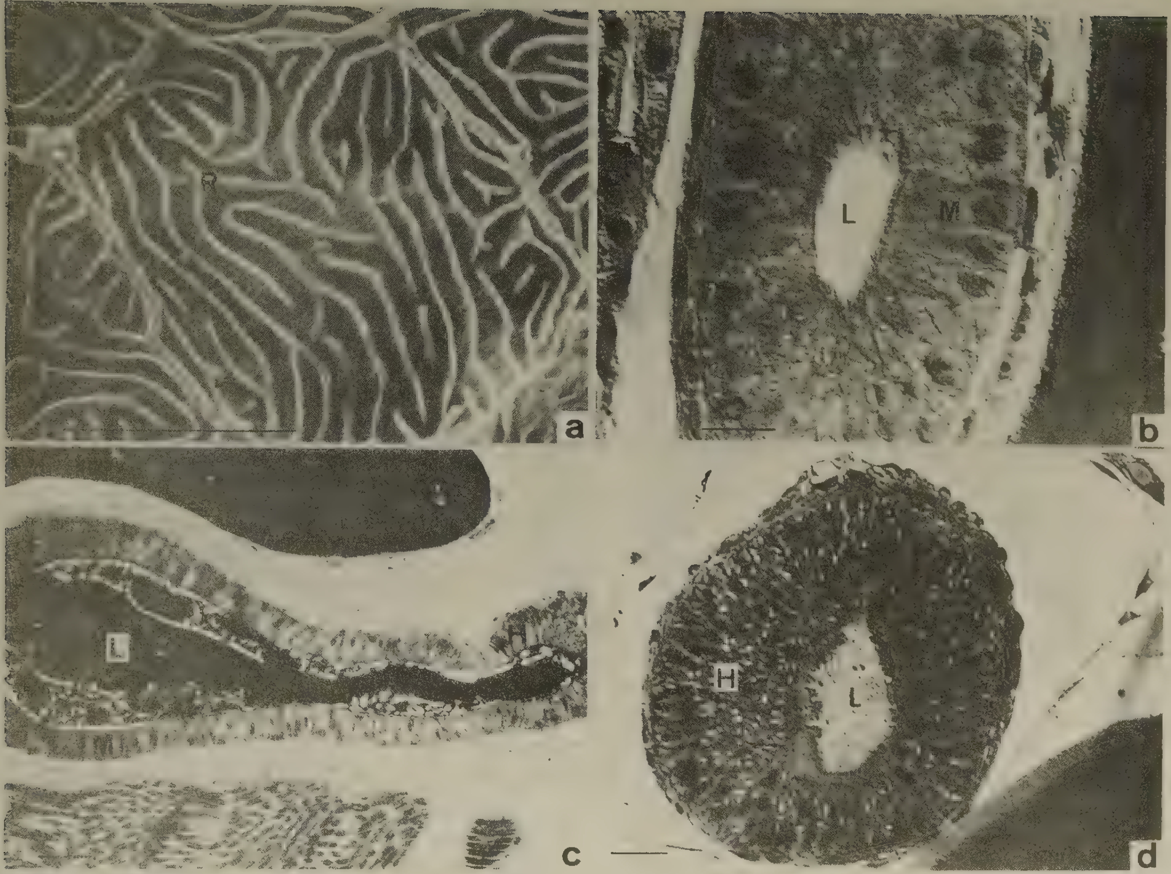

Fig. 2. Micrographs of the epidermis and gut tissue of developing embryonic states from the viviparous species *Sebastes melanops* showing the mechanism of nutrition of pre-parturition embryos. Scanning electron micrograph (*a*) of a dorsal epidermal cell just posterior of the cranium at Oppenheimer (1937) stage 31 (29 d past-fertilization, approximately 7 d before parturition). Note the well developed microridges (R) which characterize the embryonic epidermis throughout development and the absence of absorptive microvilli (scale bar is 10 μm). Photomicrograph of cross section (*b*) taken just dorsal to the yolksac (Y) of a stage 21 embryo (13 d post-fertilization). Although the midgut epithelium (M) is well developed, the lumen (L) is devoid of material (scale bar is 20 μm). Photomicrograph of a longitudinal section (*c*) of the mid- (M) and hindgut (H) of a stage 28 (11 d later than *b*). At this stage, the gut is complete and the mouth open. Note the densely stained, acidophilic substance through lumen of the gut (scale bar is 50μm). Photomicrograph of a cross-section of the hindgut of a stage 31 embryo (*d*). Note that the lumen contains an amorphous, granular substance, and that the epithelial cells have supranuclear granules (scale bar is 20 μm).

and the gut epithelium is relatively narrow (Fig. 2b). With development past stage 27 (of Oppenheimer 1937), however, observation of whole embryos and serial sections show that the gut is open and functional. The lumen now contains acidophilic, amorphous material (Fig. 2c), and the hindgut epithelium becomes markedly deeper. Additionally, there are now large, supranuclear cellular inclusions and some vacuolation (Fig. 2d). These inclusions are discussed below and are generally indicative of a functional alimentary canal. Additional physiological energetic evidence (Boehlert & Yoklavich 1984b) indicates that the embryos ingest and assimilate ovarian fluid.

The larval fore-, mid-, and hindgut are histologically and functionally distinct (Richards & Dove 1971, Tanaka 1971, Theilacker 1978, Umeda & Ochiai 1973, O'Connell 1976, 1981, Vu 1976,

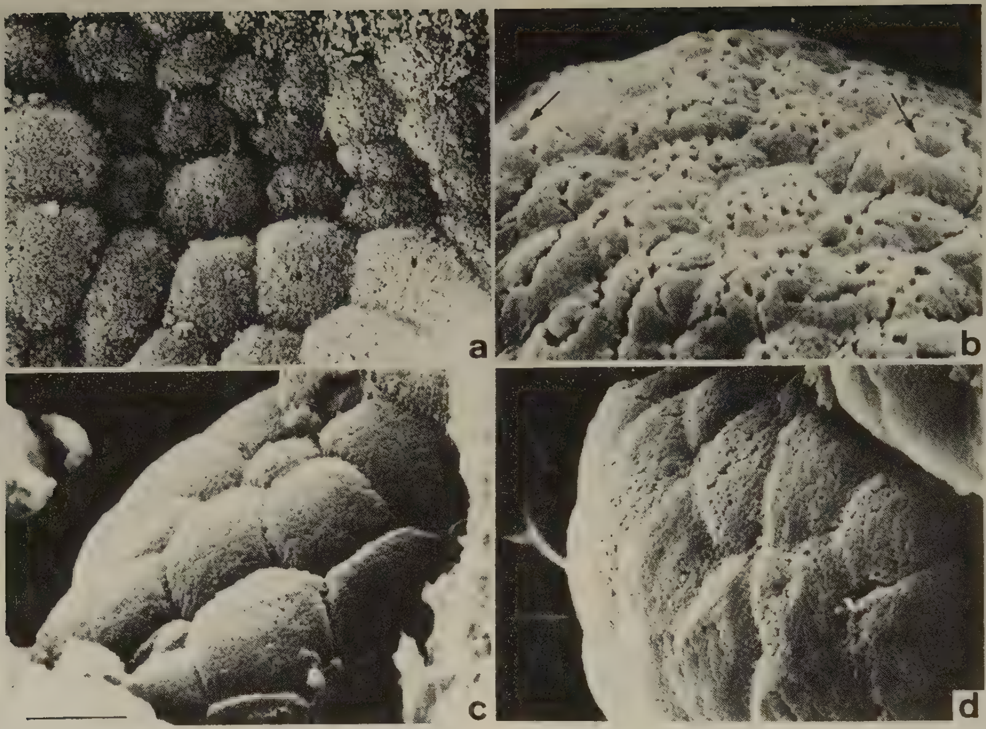

Fig. 3. Scanning electron micrographs of the apical epithelial surface of the mid- (*a*) and hindgut (*b*) of *Brevoortia patronus* larva and the mid- (*c*) and hindgut (*d*) of *Leiostomus xanthurus* larva. Note the striated border of microvilli and discharging mucous cells (arrows). (Scale bar is 5 μm; electromicrographs courtesy of J.T. Turner).

Govoni 1980, Watanabe 1981). A single layer of cuboidal epithelial cells interspersed with mucous cells lines the larval foregut. Mucous cells are more densely distributed in the anterior than in the posterior foregut of some species (Watanabe & Sawada 1985). A single layer of columnar epithelial cells with a well defined striated border of microvilli (Fig. 3) subtended by a terminal web (Fig. 4) lines the larval midgut (Iwai 1968a, 1968b, Iwai & Tanaka 1968a, 1968b, Tanaka 1971, Umeda & Ochiai 1973, Vu 1976, Stroband & Dąbrowski 1979, Stroband & Kroon 1981, Govoni 1980, O'Connell 1981, Watanabe 1982b). A single layer of columnar epithelia with microvilli (Fig. 3) and no subtending terminal web (Fig. 4) lines the larval hindgut. Mucous cells are seen in the hindgut of some species, for example gulf menhaden, *Brevoortia patronus,* while they are absent in others, for example spot, *Leiostomus xanthurus* (Fig. 3). Similarly the striated border of the hindgut in gulf menhaden is deeply furrowed, whereas it is without furrows in spot (Fig. 3).

Although not directly involved with the digestion and absorption of food, other structures, mainly the buccopharynx and the tunicae that envelop the alimentary canal, effect the processing and transport of food. At yolk absorption, the buccopharynx is lined with squamous epithelium along with scattered mucous cells and taste buds (Tanaka 1971, Govoni 1980). In relation to changes in the diets of fish larvae, taste buds become more numerous and functional as larvae grow (Twongo & MacCrimmon 1977, Appealbaum et al. 1983). Teeth develop in the areolar connective tissue underlying the buccopharyngeal epithelium, subsequently erupting during the larva period (Twongo & MacCrimmon 1977, Govoni 1980).

The dentition of fish larvae is often different

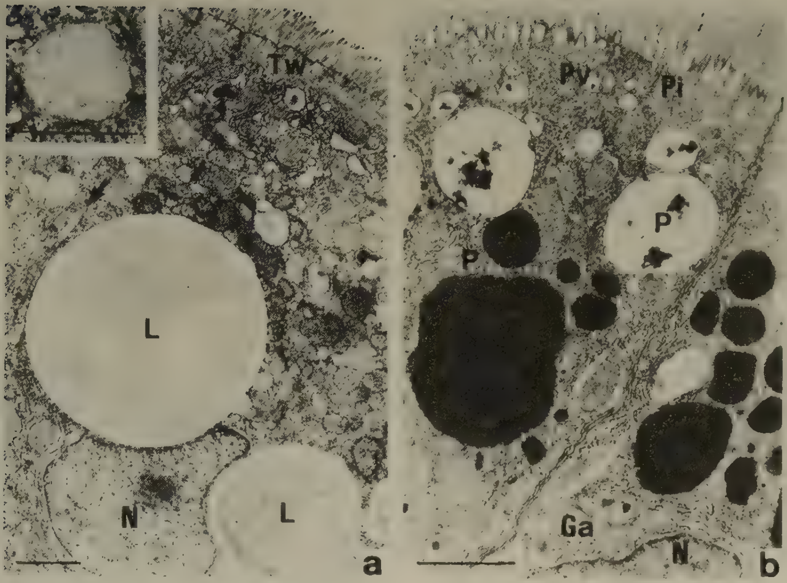

Fig. 4. Transmission electron micrographs of the mid- (*a*) and hindgut (*b*) epithelium of *Chaenogobius annularis* larva showing protein inclusion bodies (P), microvilli (MV), and terminal web (TW). Note the well defined terminal web, small, electron-lucent lipid particles (arrows), and large electron-lucent, supranuclear lipid droplets (L) in the midgut; inset is a magnification of a lipid particle. The lack of a terminal web, the presence of pinocytotic invaginations (PI) and vesicles (PV), and electron-opaque, supranuclear protein inclusion bodies are apparent in the hindgut. The lumenal, mucosal surface is in the upper right corner of each micrograph. Other abbreviations: GA, Golgi apparatus; N, nucleus. (Scale bars are 2 μm for *a* and *b*; 1 μm for inset; after Watanabe & Sawada 1985).

from that of adults, reflecting differences in feeding. For example, spot larva have retrorse conical teeth on the upper (premaxillary) and lower (dentary) jaws, but dentary teeth are lost in adults. Larval teeth are used for grasping rather than masticating food as prey are typically ingested whole.

Only three of the four enveloping tunicae typical of the adult fish alimentary canal (Kapoor et al. 1975, Reifel & Travill 1977, 1978, 1979) are present in larvae. A mucosa of absorptive epithelium, a muscularis consisting of a single layer of circular smooth muscle, and a serosa of fibrous connective tissue is present, but a muscularis mucosa or submucosa is absent until transformation. Longitudinally oriented smooth muscle in the muscularis is absent in larvae and does not develop until transformation. Whereas the longitudinal folds of the larval foregut compare well with the convolutions of the esophagus of adult fishes, the mid- and hindgut mucosa lack the distinct villi and crypt-like indentations of adults (Reifel & Travill 1979). Instead, the mucosa forms shallow rugae.

Digestive mechanisms

The function of the larval mid- and hindgut has received considerable attention inasmuch as their functions are in some ways analogous to the function of the anterior and posterior intestines of adult stomachless fishes. Moreover, there has been some controversy over the mechanisms of digestion and absorption in the mid- and hindgut (O'Connell 1976, Govoni 1980, O'Connell 1981). Cytological evidence suggests that the large supranuclear, vacuolar, electron-lucent structures of the midgut mucosal epithelial cells are the result of lipid absorption after lumenal hydrolysis to fatty acids and monoglycerides and intracellular resynthesis to lipids (Iwai 1968a, 1968b, 1969, Iwai & Tanaka 1968a, 1968b, Tanaka 1972a, 1972b, Umeda & Ochiai 1975, Stroband & Kroon 1981, Watanabe & Sawada 1985). In contrast, the acidophilic, granular, electron-opaque, supranuclear inclusion bodies of the hindgut epithelial cells are the result of pinocytotic absorption of macromolecules from the gut lumen. In addition, the terminal web underlying the striated border of the midgut shows no signs of interruption during digestion, whereas the apical plasma membrane of the hindgut shows numerous invaginations especially in recently fed larvae (Iwai 1969). Tanaka (1972b) showed that inclusion bodies become indistinct with the development of a stomach with gastric glands during transformation, but remain present in adult stomachless fishes. Govoni (1980), however, found similar supranuclear acidophilic inclusion bodies in juvenile spot that possess a functional stomach as well as in larvae that did not. Furthermore, O'Connell (1981) did not report lipid deposits in the midgut epithelial cells and found that the granular, acidophilic inclusion bodies of the hindgut epithelium stained heavily with OsO_4, a reagent that stains lipids black (O'Connell 1976).

Recently, Watanabe (1981, 1982a, 1984a), using HRP as a histochemical tracer of protein, observed pinocytotic absorption and intracellular digestion of macromolecular protein in the hindgut mucosal epithelium and revised Iwai's (1969) proposed mechanism of protein absorption. When larvae were injected with the HRP solution and their hindgut tissues incubated with H_2O_2, the epithelial cells showed HRP reaction products within inclusion bodies (Fig. 5). Control larvae showed no reaction products. It was clear that HRP was absorbed into the cells without losing enzymatic activity, i.e., without hydrolysis into peptides or amino acids.

Absorbed HRP molecules were digested in the epithelial cells through 5 successive stages: pinocytosis, transport, accumulation, digestion, and extinction (Fig. 6). Pinocytosis of HRP molecules occurred along the intermicrovillous plasma membrane. Within the cell, membrane-bounded, pinocytotic vesicles moved toward the nucleus. HRP was then accumulated in supranuclear inclusion bodies by the coalescence of vesicles. Lysosomes, presumably derived from Golgi, became associated with these inclusion bodies soon after their formation. HRP molecules in the supranuclear inclusion bodies finally lost their enzymatic activity as indicated by a waning of reaction products, probably as a result of lysosomal hydrolysis, and eventually became extinct.

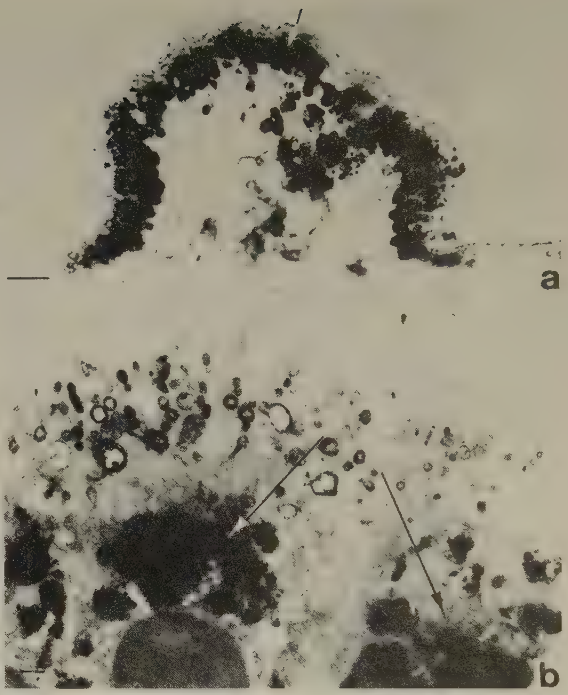

Fig. 5. Photomicrograph (*a*) and transmission electron micrograph (*b*) of the horseradish peroxidase (HRP) histochemistry of the hindgut epithelium of larval *Cottus nozawae*. Note granular and electron-opaque reaction products of HRP in pinocytotic vesicles and supranuclear inclusion bodies (arrows). (Scale bars are 30 μm for a; 1 μm for b).

The time required for complete digestion of HRP differed with species from 10 to 24 h in pond smelt, *Hypomesus transpacificus nipponensis,* to 1 to 2 weeks in cherry salmon, *Oncorhynchus masou.* The intracellular digestion time also depends on the developmental interval of fish, e.g., it was shorter in larvae than in juveniles.

Most fish larvae lack a stomach with functional gastric glands until the completion of transformation, while the larvae of some taxa develop a functional stomach before yolk absorption and first oral feeding. Secretions of gastric glands, pepsin and HCl, effect preliminary protein digestion, thereby facilitating the complete hydrolysis of proteins to peptides and amino acids through the action of trypsin, chymotrypsin, and aminopeptidase in the mid- and hindgut. One might expect greater pi-

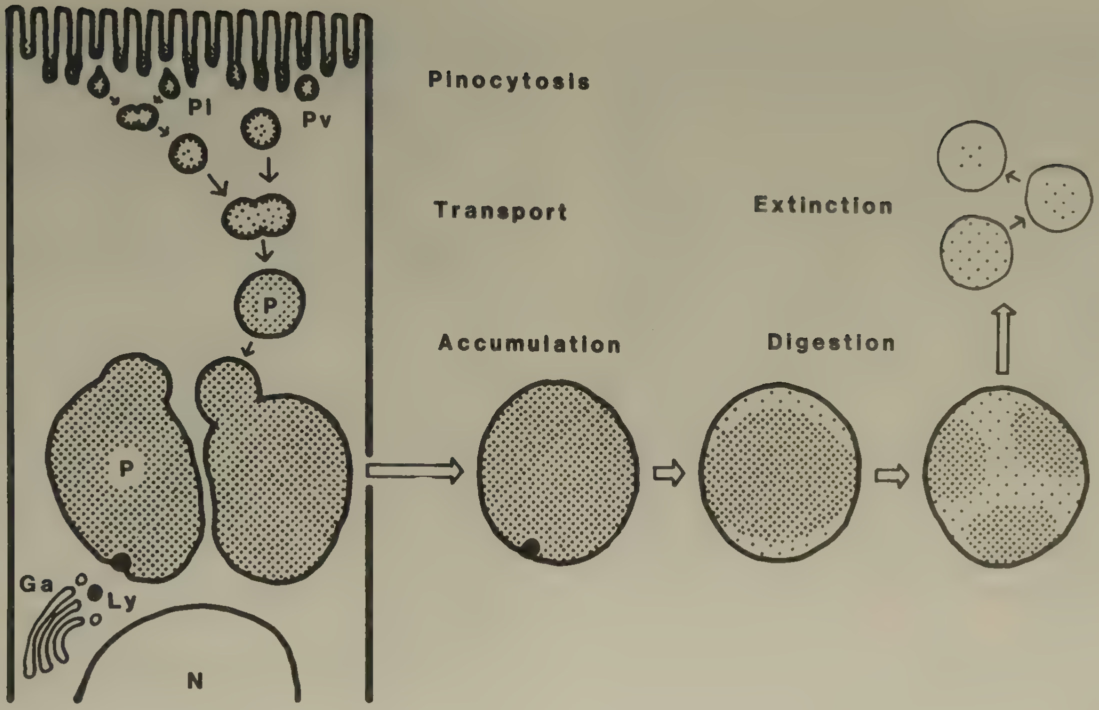

Fig. 6. Successive, 5 stages of protein absorption and intracellular digestion by the hindgut epithelial cells of fish larvae. Organelles include pinocytotic invaginations (Pi), pinocytotic vesicles (Pv), protein inclusion bodies (P), Golgi apparatus (Ga), lysosomes (Ly), and the nucleus (N). (After Watanabe 1984a).

nocytotic absorption of partially digested macromolecular proteins by the hindgut epithelial cells in fish larvae and adults that lack a stomach and preliminary protein digestion. Cherry salmon may serve as an example of a fish larvae with a functional stomach (Watanabe 1984c); pond smelt may serve as an example of a more typical fish larva without a stomach (Watanabe 1984b). Based on the absorption of HRP, the capacity to pinocytotically absorb proteins appeared before yolk absorption and first feeding in both species and persisted long after the development of gastric glands (Fig. 7). The amount of protein absorbed from food by pinocytosis, as indicated by the number of electron-opaque granules in epithelial inclusion bodies, was much greater in pond smelt larvae before gastric development than in cherry salmon larvae (Fig. 7). Pinocytotic absorption diminished in pond smelt after transformation. Pond smelt illustrated the typical pattern of fish larvae, the mechanism of protein digestion and absorption changes from pinocytosis and intracellular digestion to extracellular digestion and membrane transport with the development of gastric glands, whereas in cherry salmon, the digestive mechanism of larvae is similar to that of adults. Pinocytotic

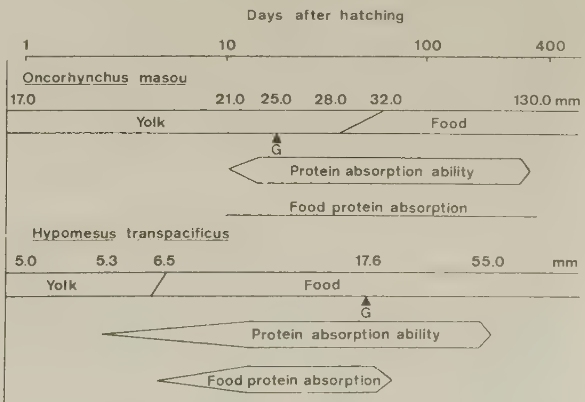

Fig. 7. Post-hatching changes in digestive mechanisms of *Oncorhynchus masou* and *Hypomesus transpacificus nipponensis* (After Watanabe 1984d).

Formation of functional gastric glands are indicated by (G).

absorption and intracellular digestion of proteins lends a possible adaptive advantage. This mechanism of digestion may compensate for incomplete digestion by allowing for the assimilation of macromolecular proteins and is apparent in the undeveloped alimentary canals of some other chordates, including some fetal and infant mammals (see reviews in Yamamoto 1982, Gauthier & Landis 1972) as well as in larvae and adult stomachless fishes (Yamamoto 1966, Kapoor et al. 1975, Noaillac-Depeyre & Gas 1976, Weinberg 1976, Stroband 1977, Stroband & Van Der Veen 1981).

Lipids are apparently digested to fatty acids and monoglycerides in the midgut lumen, absorbed into the midgut epithelium, resynthesized in the agranular endoplasmic reticulum, and deposited in large lipid droplets (sensu Watanabe & Sawada 1985) of the mucosal epithelial cells (Iwai 1969), but the exact mechanism of lipid absorption is not known. Similarly, lipids are digested and absorbed in the anterior intestine of adult fishes (Barrington 1957, Kapoor et al. 1975, Fange & Grove 1979). Lipids observed in the midgut of fish larvae and the anterior intestine of adult stomachless fishes (Noaillac-Depeyre & Gas 1974, 1976, Stroband & Debets 1978) are thought to be temporary storage (Tanaka 1972a, Stroband & Dąbrowski 1979, Watanabe & Sawada 1985).

The morphological position and mechanism of carbohydrate absorption is unexplored in fish larvae. The high densities of mitochondria in the midgut epithelial cells, some of which are associated with lipid droplets (Iwai & Tanaka 1968a, Iwai 1968b, 1969), suggest that these cells are energetically active and capable of active transport. Whether effected by non-saturable influx or by

Table 1. Digestive enzyme activities reported for fish larvae. Positive signs (+) indicate presence of enzyme activities; negative signs (–) absence; NA indicates that the enzyme was not assayed.

Species	Age range	Pepsin	Trypsin	Chymotrypsin	Amino peptidase	Lipase	Amylase	Maltase	Authors
Salmo gairdneri	first feeding to 110 d	NA	+	+	+	NA	NA	NA	Lauff & Hofer (1984)
S. gairdneri	first feeding to 66 d	+	+	NA	NA	NA	NA	NA	Dąbrowski (1982)
S. gairdneri	hatching to 60 d	+	+	NA	NA	NA	+	+	Kawai & Ikeda (1973a)
Coregonus hybrids	first feeding to 130 d	NA	+	+	+	NA	NA	NA	Lauff & Hofer (1984)
Coregonus pollan	first feeding to 42 d	+	+	NA	NA	NA	NA	NA	Dąbrowski (1982)
Plecoglossus altivelis	yolksac to transformation	+	+	NA	NA	NA	+	NA	Tanaka, Kawai & Yamamoto (1972)
Esox lucius	18 d	+	+	NA	NA	–	–	NA	Szlaminska (1980)
Cyprinus carpio	hatching to 125 d	+	+	NA	NA	NA	+	+	Kawai & Ikeda (1973b)
Gadus morhua	hatching to 30 d	NA	+	NA	NA	NA	NA	NA	Hjelmeland et al. (1983)
Acanthopagrus schlegellii	hatching to 35 d	+	+	NA	NA	NA	+	NA	Kawai & Ikeda (1973b)
Dicentrarchus labrax	hatching to 30 d	+	+	+	NA	NA	NA	NA	Alliot, Pastoureaud & Treller (1977)
D. labrax	2 to 60 d	+	+	+	NA	NA	NA	NA	Vu (1983)

sodium-dependent active transport (Crane 1975, Ferraris & Ahearn 1984), the mechanism of carbohydrate absorption is unknown.

Enzymology

Enzyme assays of the alimentary canal in fish larvae indicate that pepsin, trypsin, chymotrypsin, and amylase activities are apparent in several freshwater and marine fish larvae (Table 1). Maltase and aminopeptidase activities are present in the two species so far examined. Surprisingly, lipase activities have not been reported in the larval alimentary canal, although lipase has been assayed in only one species. The liver and the mucosal epithelium are likely the sources of lipase secretion (Kapoor et al. 1975), but zymogen granules, the histological evidence of secretory enzyme precursors, have not been reported in hepatocytes or mucosal epithelial cells of fish larvae. The pancreas is well developed at hatching in northern anchovy and spot, and its acinar cells are invested with conspicuous, acidophilic, zymogen granules, presumably the precursors of trypsin and chymotrypsin (O'Connell 1976, Govoni 1980). Aminopeptidase, another secretion of the mucosal epithelium has not been observed as zymogen. The origin of maltase is unknown in fishes (Kapoor et al. 1975). Pepsin, a secretion of the gastric mucosa, is not apparent (in those fish larvae that lack a stomach) until gastric glands in the developing stomach become functional during transformation (Tanaka et al. 1972, Kawai & Ikeda 1973b, Alliot et al. 1977, Vu 1983).

There is some indication that the activities of digestive enzymes are low at first feeding and increase during the larva period before transformation. Kawai & Ikeda (1973b) observed that activities of amylase, maltase, and trypsin increased in bulk assays of larvae of increasing age after yolk absorption. In contrast, Hjelmeland et al. (1983), using the more sensitive and specific radio-immunoassay technique, observed that after an initial increase betweeen hatching and yolk absorption, trypsin and trypsinogen activities decreased to low levels for 14 d, then increased.

There are two possible explanations for the possible increase in carbohydrolytic and proteolytic enzyme activities in fish larvae after yolk absorption and first feeding. First, the enzymes that are inherent in the food of fish larvae may increase as a result of increasing ration size. Second, enzyme production by the larval liver, pancreas, and mucosal epithelium may be stimulated in response to initial food consumption and increasing ration size. Lauff & Hofer (1984) found that exogenous trypsin activated by the high pH (9) of the hindgut of whitefish larvae, *Coregonus,* accounted for a high percentage of the total tryptic activity. Enzyme stimulation has not been observed, but the deterioration of pancreatic zymogen granules (O'Connell 1976, Theilacker 1978) and of proteolytic enzyme activities in the alimentary canal (Dąbrowski 1982, Hjelmeland et al. 1983) of starved fish larvae implies that enzyme production is variable.

Histochemistry

Beyond the histochemical application of HRP to define the mechanism of protein digestion and absorption, few studies have examined the histochemistry of the developing alimentary canal. Prakash (1961) found increasing activities of alkaline phosphatase in the striated border of the hindgut of rainbow trout, *Salmo gairdneri,* larvae with the greatest changes in the intensity of activity during transformation. Ikeda (1959) related the activities of alkaline phosphatase to the development of a functional stomach in Japanese killifish, *Oryzias latipes.* Inasmuch as alkaline phosphatase activity is associated with sodium-mediated active transport in absorptive tissues (Ugolev 1965), changes in the intensity of alkaline phosphatase reactions may indicate increased absorption through active transport.

Peristalsis and digestion rates

Constriction of the single layer of smooth circular muscle in the muscularis that progresses posteriad in a wave-like manner effects the transport of food toward the anus of fish larvae. Peristalsis is apparent in young Atlantic menhaden (*B. tyrannus*), spot, and rockfish embryos. Blaxter (1969) and

Rosenthal & Hempel (1970) reported that *Artemia* nauplii move rapidly and undigested through the midgut to the hindgut of Atlantic herring, *Clupea harengus harengus* larvae. Pedersen (1984), in contrast, observed that ingested copepods passed through the foregut of herring within seconds, passed through the anterior midgut within minutes, and stopped in the posterior midgut at the ileocaecal valve. Copepods remained in the posterior midgut and hindgut for several hours. Constrictions of the ileocaecal valve also check the transport of food from the mid- to the hindgut in Atlantic menhaden and spot larvae.

Fish larvae lack the layer of longitudinally aligned, smooth muscle in the muscularis that is characteristic of adults, but some have ancillary means of transporting food. Iwai (1964, 1967a, 1967b), Iwai & Rosenthal (1981), and Watanabe (1984b) have observed ciliated cells and cilia movement that aid in the transport of food in the alimentary canals of some plecoglossid, osmerid, clupeid, and salangid larvae. Ciliated cells have also been observed in some adult fishes with poorly developed musculari (Ferraris & Ahearn 1984).

The passage of food through the larval alimentary canal (Table 2) occurs at rates that are somewhat faster than rates observed in adult fishes (Kapoor et al. 1975, Fange & Grove 1979). Extremely

Table 2. Evacuation rates and times of fish larvae as determined in the laboratory.

Species	Age or length	Feeding protocol	Food	Temperature (°C)	Evacuation rate	Evacuation time	
Clupea harengus	12 mm		*Artemia salina*			19	Kurata (1959)
C. harengus	10 to 14 mm	Continuous feeding	*A. salina*			4 to 10	Rosenthal & Hempel (1970)
C. harengus	8 to 12 wk		*A. salina*		−0.09 to −0.84	3 to 7+	Werner & Blaxter (1980)
C. harengus	8–22 d	Single feeding	Copepod nauplii and polychaete larvae	6		12.5 to 22.5 h	Fossum (1983)
C. harengus	22–52 d	Continuous	zooplankton	9.5		40 min to 3 h	Pedersen (1984)
Coregonus clupeaformis	19–20 mm	Single feeding	Copepod nauplii	14		16	Hoagman (1974)
Cyprinus carpio						1 to 8	Chiba (1961)
Abramis brama	12–18 mm	Single feeding	*Bosmina longirostris*			5	Sorokin & Panov (1966)
Micropterus salmoides	2–8 d	Continuous feeding	zooplankton	17 to 23		2.0 to 2.8	Laurence (1971)
M. salmoides	2–8 d	Single feeding	zooplankton	17 to 23		3.8 to 5.2	Laurence (1971)
Lagodon rhomboides	15 to 18 mm	Single feeding	copepods	12	0.8		Kjelson & Johnson (1976)
Leiostomus xanthurus	16 to 20 mm	Single feeding	copepods	17	0.24		Kjelson & Johnson (1976)
L. xanthurus	7 to 47 d 1.8 to 9.4 mm	Single feeding	*Brachionus plicatilis*	20		5 h	Govoni et al. (1982)
Scomber japonicus	3–5 d	Single feeding	*B. plicatilis*	19	0.5 to 2		Hunter & Kimbrell (1980)
Pseudopleuronectes americanus		Continuous feeding	zooplankton	8		5.1 to 8.4	Laurence (1977)

rapid rates have been observed with some clupeoid larvae. In one report, bay anchovy, *Anchoa mitchilli*, defecated within minutes after eating (Chitty 1981). In Atlantic menhaden and spot larvae, however, defecation begins 1 to 2 h after eating. Larval age does not markedly affect the evacuation rate of herring larvae (Pedersen 1984). Evacuation rates are faster for larvae fed continuously than for larvae fed a single ration (Blaxter 1965, Laurence 1971) and are positively related to ration size (Werner & Blaxter 1980). Evacuation rates are also positively related to temperature (Laurence 1971). In any case, digestion and assimilation in fish larvae are rapid. By visual inspection, Fossum (1983) observed the digestion of copepod nauplii and polychaete larvae within 1.5 h following their ingestion by Atlantic herring larvae. Govoni et al. (1982) observed that larvae respired $^{14}CO_2$ within 3 h following the ingestion of ^{14}C-labeled food, which indicates that food is digested, assimil-

Table 3. Assimilation efficiencies and the coefficient of utilization of fish larvae.

Species	Age, length or weight	Food	Food concentration	Method of determination	Assimilation efficiency (%)	Coefficient of utilization (%)	Author
Anchoa mitchilli	10 to 100 μg dry weight	Copepod nauplii	1000 1^{-1}	gravimetric		24 to 41	Houde & Schekter (1983)
Clupea harengus	6 wk	*Artemia salina*	10^{-6} to 10^{-3} 1^{-1}	radiotracer (^{14}C)		38 to 68	Boehlert & Yoklavich (1984a)
Cyprinus carpio	1–5 mg dry weight	zooplankton	10 to 100 mg 1^{-1}	calorimetric	74 to 87		Filatov (1972)
Abramis brama	12 to 18 mm	*Bosmina longirostris*	20 to 2000 l^{-1}	radiotracer (^{14}C)	74 to 83		Sorokin & Panov (1966)
Micropterus salmoides		zooplankton	200 to 1200 l^{-1}	calorimetric		80	Laurence (1971)
Archosargus rhomboidalis	10 to 100 μg dry weight	copepod nauplii	500 1^{-1}	gravimetric	44 to 75		Houde & Schekter (1983)
Leiostomus xanthurus	7 to 47 d 1.8 to 9.4 mm 0.022 to 2300 μg dry weight	*Brachionus plicatilis*	10^5 to 10^6 l^{-1}	radiotracer (^{14}C)	67 to 99	9 to 65	Govoni et al. (1982)
Paralichthys dentatus	1 to 56 d	zooplankton	unlimited	nitrogen assay		27 to 68	Buckley & Dillman (1982)
Limanda limanda	0 to 32 d	oligochaetes unlimited calorimetric	unlimited		99		Calculated from Edwards et al. (1969)
Pleuronectes platessa	0 to 45 d	ologochaetes unlimited calorimetric	unlimited		96 to 99		Calculated from Edwards et al. (1969)
Pseudopleuronectes americanus	16 to 668 μg dry weight	copepod nauplii	2000 to 3000 l^{-1}	calorimetric		69 to 74	Laurence (1977)
P. americanus	16 to 23 d	zooplankton	>2000 1^{-1}	nitrogen assay		20	Cetta & Capuzzo (1982)
Achirus faciatus	10 to 100 μg dry weight	copepod	1000 l^{-1}	gravimetric		34 to 54	Houde & Scheckter (1983)

ated, and metabolized within this short period.

Assimilation

Mass and energy budgets (physiological energetics) as well as radiotracer experiments indicate that the assimilation efficiency of fish larvae (Table 3) is near or somewhat below the assimilation efficiency of adult fishes (Kapoor et al. 1975, Conover 1978, Brett & Groves 1979). Assimilation efficiency (the percentage of a food ration that is assimilated after loss to feces (Brett & Groves 1979)) ranges from 67 to 99% for fish larvae, whereas assimilation efficiency ranges from 80 to 90% for adults. Coefficients of utilization (the fraction of matter or energy retained after losses to defecation of feces as well as metabolic excretion of urine (Winberg 1956)) for fish larvae are also generally lower than they are for adults. The coefficients of utilization ranges from 9 to 80% for larvae, whereas coefficients average about 70% for adults (Ware 1975).

The effects of food type and ration size on assimilation efficiencies are poorly known for fish larvae. In stomachless pipefish larvae, *Syngnathus fuscus*, Ryer & Boehlert (1983) noted slower evacuation with smaller ration and suggested that assimilation efficiency would increase at low ration when the residence time of individual food particles increased. In Atlantic herring larvae, Werner & Blaxter (1980) observed that high rations resulted in food that was apparently less digested when defecated; indeed, at the highest ration, *Artemia* nauplii passed rapidly through the alimentary canal and were defecated alive. This observation coupled with the extremely rapid evacuation times in bay anchovy larvae (Chitty 1981) implies that large rations may result in low assimilation efficiencies, especially for clupeoid larvae with straight alimentary canals. This has been experimentally confirmed for Pacific herring larvae, *C. harengus pallasi*; the uptake and retention of ^{11}C-labeled food decreased significantly with increasing food concentration and, therefore, ration (Boehlert & Yoklavich 1984a). Herring larvae have straight guts. It would be of interest to repeat these experiments to determine if percoid larvae with coiled guts show the same change in assimilation efficiency, inasmuch as the feeding strategies of species with differing gut morphologies may differ, as demonstrated by the work of Houde & Schekter (1980, 1983). The clupeoids are adapted to utilize contagiously distributed prey in high concentrations; although assimilation efficiency and gross growth efficiency may decrease, the total energy intake increases (Fig. 8), resulting in a net energetic gain to the larva. Similarly, comparing a wide variety of fish larvae, Checkley (1984) noted that gross growth efficiency showed a peak at moderate food densities and decreased thereafter, a pattern similar to adult fishes (Brett & Groves 1979).

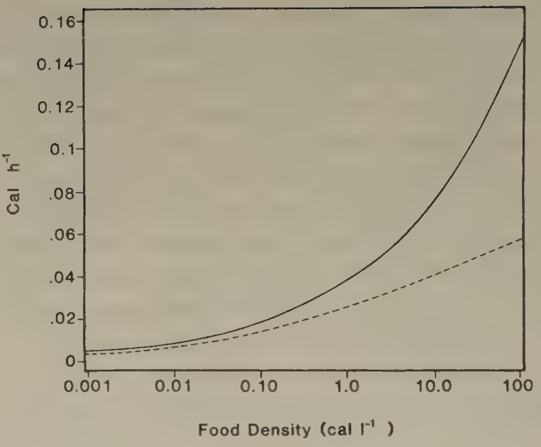

Fig. 8. The relationship of calories consumed (solid line) and calories assimilated (dashed line) as a function of food density for 6 wk-old *Clupea harengus pallasi* larva feeding on *Artemia* nauplii. Ingestion rate increases with food density for this species (Werner & Blaxter 1981). Although assimilation efficiency decreases with increasing ingestion rate, the magnitude of decrease with increasing ingestion rate is more than compensated for by increased ingestion such that the total energy assimilation continues to increase. (From Boehlert & Yoklavich 1984a).

Some work has indicated that the low assimilation efficiencies of some fish larvae improve during the larva period, while other research has failed to demonstrate improved efficiencies until transformation with its attendant elaboration of alimentary canal morphology. By subtracting the amount of energy in growth and metabolism from the energy in food, Laurence (1977) reported increasing assimilation efficiencies during the larva period before transformation. In contrast, Sorokin & Panov (1966) and Govoni et al. (1982), by using ^{14}C as a tracer, and Houde & Schekter (1983), by subtracting the energy of growth and metabolism from the energy of food, reported no change in assimilation with development before transformation in several other species. Buckley & Dillmann (1982) measured the nitrogen excreted as ammonia in urine and defecated as primary amines in feces by summer flounder larvae, *Paralichthys dentatus*. They reported that the rate of defecation of primary amine, representing the nonassimilated fraction of ingested nitrogen, decreased with age, while the rate of ammonia, representing the assimilated and metabolized fraction, decreased until 35 h after hatching, then increased. More importantly, the coefficient of nitrogen utilization increased with age during the larva period. Cetta & Capuzzo (1982) found a similar pattern of nitrogen loss in the larvae of another flatfish, *Pseudopleuronectes americanus*. Pinocytosis and intracellular digestion of protein macromolecules is possibly a less efficient mechanism of protein digestion and assimilation than hydrolysis to amino acids and active transport across the lumenal plasma membrane (Gardner 1984). While this might account for the overall lower assimilation efficiencies of the fish larvae, what accounts for changes in assimilation during the larva period before transformation? Some of proteolytic enzymes indicate that enzyme activities increase during the larva period before transformation, and Buckley & Dillmann (1982) invoked these increases to explain increasing assimilation. This explanation is plausible, but there is no corresponding cytological evidence of an increase in the capacity of the pancreas to produce these enzymes; the pancreas has conspicuous zymogen granules at yolk absortion and these remain obvious throughout development. This lack of apparent morphological or cytological change that could cause a shift in the efficiency of digestion and assimiltion is puzzling.

Improvement of assimilation efficiency is likely with the development of a functional stomach with gastric glands and pyloric caeca at transformation due the digestive contribution of pepsin and hydrochloric acid and the increased absorptive surface area of the alimentary canal. Mironova (1974) reported increasing assimilation efficiency of *Oreochromis mosambicus* that was concomitant with transformation.

Recommendations for future research

We know that the alimentary canal of fish larvae is less complex than that of adults and that digestion and assimilation in larvae may be less efficient as a result. The activities of proteolytic enzymes are apparently lower in larvae, but may increase as larvae grow before transformation. In some flatfish larvae, nitrogen assimilation improves during the larva period, but measures of calorie and carbon assimilation with larvae other than flatfish have indicated no improved assimilation before transformation. For most fish larvae there is no apparent elaboration of alimentary canal tissues after yolk absorption and before transformation; alimentary canal development is not well studied among flatfish.

Research on the physiology of digestion in fish larvae has faced several technical difficulties. The small size of larvae, their mostly planktonic habitat, and the unavailability of natural prey sources to experimenters, among other problems, have all contributed variability to the range of results reported herein. Consequently, several questions remain to be answered. Inasmuch as it has bearing on models of larval growth and survival, the question of changing digestive and assmilative abilities with larval development before transformation warrants the most immediate attention. Several avenues of research to address this issue are possible.

The length as well as the absorptive surface area of the alimentary canal should be measured and related to larval length. The morphometric methods of Hughes (1984) could be used for this purpose. Such comparisons would indicate disproportionate increases in the absorptive surface area with development and might offer an explanation for improving assimilation.

A histochemical examination of developmental stages of various species should also contribute to the resolution of changing assimilation. Such an examination should focus on lipase and esterase because histochemical evidence of these enzymes would indicate the capability of larvae to digest and absorb lipids. The histochemistry of alkaline phosphatase, because of its association with sodium-mediated active transport, and acid phosphatase, because of its association with supranuclear inclusion bodies and pinocytotic absorption (Ugolev 1965, Watanabe 1984a), should also be considered. We recommend the histochemical methods of Higuchi et al. (1979) with the intensity of histochemical reactions quantified with image-analysis densitometry.

The question of enzyme stimulation should be resolved by conducting carefully controlled experiments wherein developmental stages of different species are starved and then fed for various intervals, and the activities of digestive enzymes measured. Because of its sensitivity in distinguishing specific antibody and antigen reactions and its capacity to detect inhibited as well as active trypsin, we recommend radio-immunoassay (Hjelmeland 1983, Hjelmeland et al. 1983) for measurement of trypsin activities. Perhaps radio-immunoassays could be developed for other digestive enzymes.

A comparative approach to these recommendations would be clearly advantageous, for morphological and physiological differences among taxa are great. Studies on digestive physiology elucidate the feeding strategies and growth potential of fish larvae and thereby contribute to our understanding of fish larvae survival.

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Mitochondrial DNA Genetic Similarity of Atlantic and Pacific Skipjack Tuna and Its Management Implications

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Restriction enzyme analysis of mitochondrial DNA (mtDNA) provides the most powerful, practical tool currently available for determining the genetic basis of population structure. This technique applied to skipjack tuna from the Atlantic and Pacific Oceans demonstrated no significant genetic differentiation between fish from different ocean basins although within-sample variation was detected. These results are consistent with the lack of morphological and electrophoretic differentiation of Atlantic and Pacific skipjack tuna found in previous studies and strongly suggest sufficient gene flow between ocean basins to prevent genetic differentiation. As no significant genetic differentiation was exhibited between Atlantic and Pacific skipjack tuna it is unlikely that genetically distinct stocks exist within the Atlantic Ocean. Consequently, any subdivisions of Atlantic skipjack into management units will have to be based upon non-genetic criteria.

L'analyse de l'ADN mitochondrial (ADNmt) par les enzymes restrictifs est la méthode la plus efficace et pratique actuellement disponible pour déterminer la base génétique de la structure de la population. Cette technique, appliquée au listao des océans Atlantique et Pacifique, n'a pas montré de différenciation génétique significative entre les poissons de différents bassins océaniques, mais une variation a été décelée entre les échantillons. Ces résultats concordent avec le manque de différenciation morphologique et électrophorétique entre listaos de l'Atlantique et listaos du Pacifique qui a été observée dans les études antérieures, et donnent de fortes raisons de penser que l'échange de gènes entre les bassins océaniques est suffisant pour empêcher une différenciation génétique. Aucune différenciation de cette nature n'ayant été observée entre les listaos de l'Atlantique et ceux du Pacifique, il est peu probable qu'il existe dans l'Atlantique des stocks distincts du point de vue génétique. Toute subdivision du listao de l'Atlantique en unités de gestion devra donc se baser sur des critères non-génétiques.

El análisis del DNA mitocondrial (mtDNA) empleando enzimas restrictivas es en la actualidad el método más adecuado y práctico para determinar la base genética de la estructura de la población. Esta técnica, aplicada al listado del Atlántico y del Pacífico, demostró que no había una diferenciación genética importante entre los peces de los dos océanos, si bien se observó variación entre las muestras. Estos resultados concuerdan con la falta de diferenciación morfológica y electroforetica del listado del Pacífico y del Atlántico, encontrada en anteriores estudios y sugiere categóricamente la existencia de una corriente genética. Al no encontrarse esta diferenciación entre el Atlántico y el Pacífico, es poco probable que existan stocks genéticamente distintos dentro del Atlántico. Por tanto, cualquier subdivisión del listado atlántico en unidades de ordenación deberá estar basada en criterios no-genéticos.

1. Introduction

The concept of the unit stock is fundamental to fisheries biology. Clearly, if all exploited fish species were composed of genetically isolated, intraspecific groups which were self-sustaining and independently vulnerable to the effects of fishing, fisheries management would be considerably simplified. However, as there are almost as many different types of underlying population structures as there are exploited species, it is unrealistic to assume that the unit stock concept is applicable to all fisheries.

Exploited fish species have intraspecific population structures that fall along a continuum from species with discrete unit stocks to panmictic species which demonstrate no intraspecific population structure at all (random mating). For example, the Atlantic herring displays an intraspecific population structure close to the unit stock concept (Iles and Sinclair 1982), whereas some pelagic fishes (sauries, billfishes) may almost be panmictic. To effectively manage a fishery one must have a clear understanding of the population structure of the exploited species.

The nature and amount of gene flow within and between intraspecific groups determines population structure. However, because gene flow is difficult to measure most fisheries investigators of population structure search for intraspecific genetic differentiation which results from an absence or severe reduction of gene flow. Thus, genetic differentiation, or more properly, the phenotypic expression of genetic differentiation, has provided the basis for most fisheries analyses of population structure.

Phenotypic characters used to distinguish intraspecific populations must have a strong genetic basis. Many characters typically used to differentiate populations or stocks, such as morphometrics, meristics, reproductive features (spawning season, fecundity), growth rates, etc., may have a strong genetic basis — yet their expression can be strongly influenced by the environment. A large environmental influence on any character used to infer genetic relationships can lead to spurious conclusions. For example, fish of different genetic and geographic origins living in cool water might have slower growth rates than those living in warmer water. An analysis of growth rates of these fish would indicate significant differences in growth rates but would provide no significant genetic information. Thus, caution must be used when inferring genetic information from phenotypic data.

When discriminating or identifying stock units with phenotypic or genotypic characters, two criteria must be met: (1) the character used must show enough pooled intraspecific variation to allow discrimination of stocks and (2) there must be sufficient differentiation between stocks to allow identification with practical sample sizes. Some characters, though highly variable, will not differentiate stock units.

Much effort has been made to elucidate the genetic basis of population structure of skipjack tuna (*Katsuwonus pelamis*) using meristic, morphometric, growth, reproductive and electrophoretic characters (reviewed in Argue 1981). These studies have detected little character variation among skipjack tuna, and as a result have demonstrated only slight differentiation between individuals from different ocean basins. The small amount of intraspecific differentiation in genetic characters studied could either be attributed to strong selection resulting in the conservation of the analyzed characters or sufficient gene flow between ocean basins to prevent differentiation. To distinguish between the alternatives of character conservation or gene flow is difficult — one must search for additional characters with enough intraspecific variation to detect differentiation if it exists, or ultimately to accept the null hypothesis of no stock separation (gene flow between sampling locations).

This paper presents the results of a restriction endonuclease analysis of mitochondrial DNA (mtDNA) of skipjack tuna from the Atlantic and Pacific Oceans. Restriction enzyme analysis is currently the most powerful genetic technique available to population biologists for determining the genetic basis of intraspecific differentiation. This study was undertaken to determine if significant interocean genetic differences exist between skipjack, and to determine if further genetic analyses within the Atlantic Ocean are warranted.

2. mtDNA Analysis

The characters investigated in population analyses often differ greatly in the level and complexity of their underlying genetic basis as well as the degree to which they are susceptible to environmental influence. Most morphological, meristic, growth, and reproductive characters are the result of the interaction of several distinct genetic loci and some degree of environmental influence. Electrophoretic and immunogenetic characters are usually the products of one or a few genetic loci and are typically, but not completely, free from environmental influence. Only by investigating the actual genetic material (DNA) can one be sure of avoiding the problems of environmental modification.

The structure, function and evolution of the nuclear genome (nuclear DNA) are not well known. As a result, it is difficult to compare nuclear genomes of organisms for genetic studies. On the other hand, the mitochondrial genome (mtDNA) provides a very tractable molecule for comparative genetic analyses (Avise et al. 1979a). mtDNA is a small molecule and unlike nuclear DNA is maternally inherited and does not undergo recombination during meiosis (Giles et al. 1980). The complete nucleotide sequences of mouse, cow and human mtDNAs have recently been published (Bibb et al. 1981; Anderson et al. 1981, 1982). These and other sequence studies have demonstrated that while both the function and order of the mitochondrial genome are highly conserved in vertebrates, there appears to be considerable inter- and intraspecific variation of the nucleotide sequence (Brown et al. 1982).

Sequencing the mitochondrial genome is a costly and time consuming process which is currently not practical for population studies. However, the sequence of the mitochondrial genome can be investigated with restriction endonucleases, enzymes which recognize specific 4, 5 or 6 nucleotide base pairs on the DNA and consistently cleave (break) the DNA molecule at or near the recognition site. Nucleotide substitutions in the 4, 5 or 6 base pair recognition site result in the loss of the cleavage, and consequently, a reduction in the number of fragments (Figure 1). Similarly, base pair substitutions outside of the recognition site may create a new cleavage site and mtDNA fragment. After digestion with a restriction enzyme, mtDNA fragments are separated by size electrophoretically and the fragment patterns of the individual mtDNAs digested with the same restriction enzyme are compared. The loss or gain of a fragment (cleavage site) is considered to be the result of a single base pair substitution. Typically, several different restriction endonucleases are used in a population analysis and a minimum percentage mtDNA sequence divergence between individuals is calculated from the fragment patterns using established methods (Lansman et al. 1981; Nei and Tajima 1981).

mtDNA restriction enzyme analyses have demonstrated rapid nucleotide sequence evolution both at the inter- and intraspecific level. The rate of mtDNA evolution appears to be approximately ten times faster than that of single copy nuclear DNA (Brown et al. 1982). Results from studies within several classes of vertebrates have shown that individuals from the same population tend to have very similar mtDNA sequences while individuals from geographically disjunct populations exhibit some mtDNA sequence divergence (Avise et al. 1979a, b). These differences

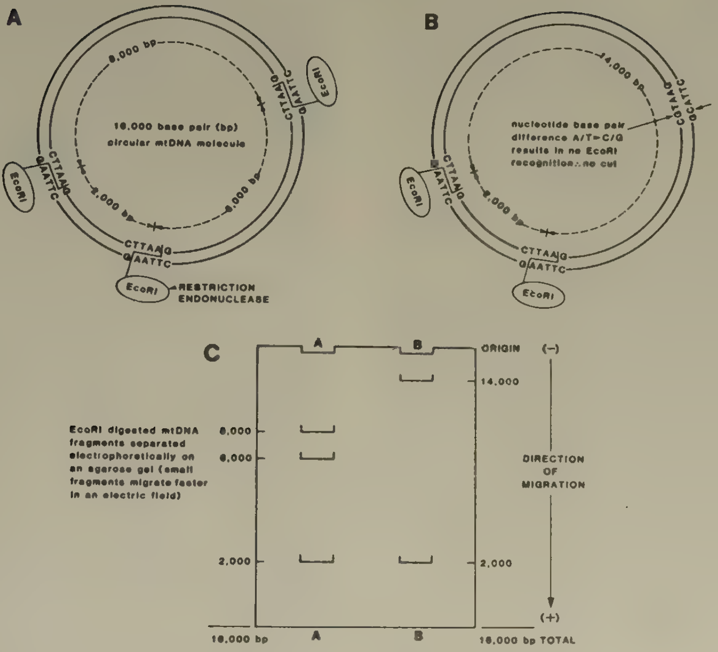
A
8,000 bp
16,000 base pair (bp)
circular mtDNA molecule
CTTAAG
GAATTC
EcoRI
2,000 bp
6,000 bp
RESTRICTION
ENDONUCLEASE
B
14,000 bp
nucleotide base pair
difference A/T→C/G
results in no EcoRI
recognition∴no cut
CTTAAG
GCATTC
2,000 bp
C
A
B
ORIGIN
(–)
14,000
EcoRI digested mtDNA
fragments separated
electrophoretically on
an agarose gel (small
fragments migrate faster
in an electric field)
8,000
6,000
2,000
DIRECTION
OF
MIGRATION
2,000
(+)
16,000 bp
A
B
16,000 bp TOTAL

Figure 1. Restriction endonuclease analysis of mitochondrial DNA (mtDNA)

The mtDNA molecule is a double-stranded, circular chain of four nucleotide bases: adenosine (A), thymine (T), cytosine (C) and guanine (G). In the double-stranded DNA chain the nucleotide bases A and T align opposite each other on the two strands, as do C and G. Vertebrate mtDNA molecules consist of approximately 16,000 nucleotide base pairs. The information of the molecule is contained within the specific sequence of the nucleotide bases. Genetically similar individuals have similar mtDNA nucleotide sequences.

In our analysis of mtDNA of Atlantic and Pacific skipjack tuna we employed restriction endonucleases to compare the similarity of mtDNA sequences of fish from the two oceans. Restriction endonucleases are enzymes that recognize specific 4, 5 or 6 nucleotide base pair sequences of the DNA molecule and consistently cut (cleave) the DNA chain at or near the recognition site. Consequently, by comparing the mtDNA fragments of individuals after treatment with restriction endonucleases (digestion), we were able to infer differences or similarities in the mtDNA nucleotide sequence.

In this figure the restriction endonuclease EcoRI, which recognizes the nucleotide sequence GAATTC, encounters three sites to cleave the circular mtDNA of fish A (A). A genetic difference (base pair change) in the mtDNA of fish b has resulted in the loss of one EcoRI cleavage site (B). Consequently, digestion of mtDNA from these two fish with the restriction endonuclease EcoRI results in three mtDNA fragments from fish A and only two from fish B. The mtDNA fragments are separated by size on agarose gels with an electric current and visualized by direct staining or with radioactive labels (C). Genetically similar fish have similar restriction endonuclease digestion patterns while less related fish share fewer bands. Skipjack tuna from the Atlantic and Pacific Oceans have strikingly similar restriction endonuclease digestion patterns. This similarity strongly suggests that they have continued to have genetic contact (interbreed) since the uplift of the Panama land bridge.

become more pronounced at the subspecies and species level. The optimal resolution of mtDNA sequence differences occurs for populations which have been separated for 0.25 to 5 million years (Brown et al. 1982).

3. Results

In our laboratory at the Southwest Fisheries Center, National Marine Fisheries Service, we have applied restriction enzyme analysis of mtDNA to skipjack tuna from the Atlantic and Pacific Oceans (Dizon et al. 1983). Our investigation of seven Atlantic (one Ponce, Puerto Rico; six Rio de Janeiro, Brazil) and nine Pacific specimens (all from Honolulu, Hawaii) with nine restriction enzymes produced a total of 39 or 40 fragments per individual. Although intraspecific variation was demonstrated with four of the nine restriction enzymes (Table 1), none of the variants were consistently present in fish from one ocean and not in the other. Thus, a genetic analysis which surveyed 1% of the skipjack mitochondrial genome demonstrated a mtDNA nucleotide sequence divergence of 0% between fish from the Atlantic and Pacific Oceans.

Table 1. Restriction endonucleases employed and the resultant patterns observed in skipjack tunas. Two types of analyses were performed: (1) mtDNA was purified and fragments were end-labelled with radioactive deoxynucleotides to enhance visualization of the gel. (2) Southern transfers of total genomic DNA were hybridized with a probe made from salmonid mtDNA. Abbreviations: HI = Hawaiian, PR = Puerto Rican and BRZ = Brazilian samples; numbers of individuals tested in parentheses; w = "wild" type (common pattern), var = "variant" type (mutated pattern).

	Restriction Patterns			
	HI	PR	HI	BRZ
Enzyme	(3 pooled)	(1)	(6)	(6)
type	(purified mtDNA)		(Southern method)	
Hind III	w	w	—	—
Hpa II	w	w	w	w
Mbo I	w	w	—	—
Pst I	w	var	w	w
Eco RI	w	w	—	—
Xba I	w	w	—	—
Sac I	w, var	—	w	w
Pvu II	w	—	w	w, var
Ava II	w, var	—	w	w

4. Discussion

As previously mentioned, for a genetic character to be a useful marker in population analyses, it must demonstrate sufficient pooled intraspecific variation to allow stock unit differentiation. Four of the nine restriction enzymes employed in this study showed intraspecific variation. Although there are presently no data from other fishes with which to compare our results, they can be compared with results from mammals surveyed with the same restriction enzymes. mtDNA restriction analysis of ten common chimpanzees with five restriction enzymes produced a total of ten variants (Ferris et al. 1981) while eight variants were found in sixteen skipjack tuna with the same enzymes. Thus skipjack tuna appear to be about one-half as variable as chimpanzees. Relative to population analyses of chimpanzees and other mammals, it would appear that sufficient mtDNA variation is exhibited by skipjack tuna to differentiate major intraspecific groups if they exist (Avise et al. 1979a, b; Lansman et al. 1981).

In the vertebrates studied to date, mtDNA appears to evolve at a rate of approximately 0.015 substitutions per nucleotide base pair per million years (Brown et al. 1982). If skipjack tuna of the Atlantic and Pacific Oceans have been separated since the uplift of the Panama land bridge some 3.1 million years ago (Keigwin 1978, 1982), one would expect a nucleotide sequence divergence of about 4–5%. Our analysis of 169 nucleotide base pairs deomonstrated a mtDNA sequence divergence of 0%. Even if a fragment were found to be present in Atlantic skipjack tuna and absent in Pacific fish with the use of one additional restriction enzyme, the sequence divergence between Atlantic and Pacific fish would only be 0.6%. It would therefore appear that skipjack tuna from the Atlantic and Pacific Oceans have not been genetically isolated since the rise of the Isthmus of Panama.

This is not the first study to report considerable genetic similarity between Atlantic and Pacific skipjack tuna. In a series of electrophoretic and immunogenetic studies, Fujino and coworkers have demonstrated a high degree of genetic similarity between fish from the two oceans (Fujino and Kang 1968; Fujino 1970a; Fujino et al. 1981). These studies report slight allele frequency differences at a few genetic loci which can be used to distinguish Atlantic and Pacific skipjack tuna providing one has large samples. However, no electrophoretic characters were found to be fixed for different alleles in fish from the two oceans; hence, it is not possible to differentiate individual fish.

The magnitude of the electrophoretic and immunogenetic differences between skipjack tuna from the Atlantic and Pacific Oceans is minute when compared to other conspecific fishes separated by the Isthmus of Panama. Tropical marine shorefishes on either side of the Panama land bridge, whether considered the same or very closely related species, exhibit between-ocean genetic distances an order of magnitude greater than those reported for skipjack tuna (Vawter et al. 1980). While 20–40% of the electrophoretic loci are fixed for different alleles between pairs of shorefishes on either coast of Panama, skipjack tuna exhibit no fixed allelic differences (Fujino 1970). It is significant that the dolphin fish (*Coryphaena hippurus*), a strictly pelagic species, is similar to the skipjack tuna in that no fixed allelic differences can characterize a fish as being from the Atlantic or Pacific Ocean and only slight allele frequency differences are found at a few loci (R. Rosenblatt and R. Waples, Scripps Institution of Oceanography, pers. com.).

The striking lack of genetic differentiation between Atlantic and Pacific skipjack tuna and dolphin fish, in contrast to the highly differentiated shorefishes, strongly suggests that there has been sufficient gene flow between ocean basins to prevent genetic differentiation of the pelagic species. The most plausible route for genetic interchange of tropical and subtropical, pelagic populations is around the Cape of Good Hope. Seasonal isotherms indicate that suitable water temperatures exist for migration of skipjack tuna and other warm water pelagic species around the Cape of Good Hope throughout most of the year (Davies 1963). Furthermore, Japanese longline data (Silas and Pillai 1982) and South African commercial and sport fishery data indicate that skipjack tuna are seasonally abundant in waters around the Cape of Good Hope (S. Grant, Sea Fisheries Institute, South Africa, pers. com.).

Skipjack tuna are capable of swimming long distances. Although not long lived fish, tagging studies have shown some individuals to travel thousands of kilometres (reviewed in Argue 1981). If skipjack tuna are capable of crossing ocean basins as tag recovery data indicate, then it is most likely that they are also able to migrate between ocean basins. Furthermore, as skipjack tuna usually travel in large schools, the potential exists for significant gene flow between ocean basins.

Genetic differentiation can occur only if there is reproductive isolation between populations. Skipjack tuna do not have distinct spawning areas and behavioral isolation has not been reported. Ripe fish and larvae are found circumtropically in warm, pelagic waters (reviewed in Sund et al. 1981). Fish swimming across or between ocean basins can mate with fish from local or distant geographic areas. The lack of reproductive isolation of skipjack tuna populations increases the possibility for significant gene flow both within and between ocean basins.

The lack of significant mtDNA sequence differentiation between Atlantic and Pacific skipjack tuna is consistent with the natural history of the fish. The existence of suitable habitat for passage around the Cape of Good Hope, the strong swimming ability of the fish (Miyabe and Bard this volume; Argue et al., this volume), and the lack of discrete spawning areas (Cayré et Farrugio this volume) all promote gene flow within and between ocean basins. The effects of this gene flow are also reflected in the high degree of morphological and electrophoretic similarity of skipjack tuna from different ocean basins.

The purpose of this study was to apply a new, high resolution genetic technique to the problem of identifying the stock structure of skipjack tuna. The sixteen fish examined in this study demonstrated intraspecific variability of mtDNA restriction sites but did not display consistent sequence differentiation between ocean basins, a finding which is consistent with those of previous genetic studies. These results do not prove that all skipjack are genetically similar; rather, they demonstrate a high degree of genetic similarity between fish from the Atlantic and Pacific Oceans which suggests sufficient gene flow to prevent significant genetic differentiation. Although some intraspecific genetic differentiation may be uncovered as more of the mtDNA genome is surveyed (more nucleotide base pairs as opposed to more individuals), at this time there are no data to suggest that skipjack exist other than as a single, genetically homogeneous, circumtropical stock.

As significant genetic differentiation has not been demonstrated between Atlantic and Pacific skipjack tuna it is unlikely that marked differentiation exists between skipjack within the Atlantic Ocean. This does not exclude the possibility of dividing the skipjack tuna stock for management purposes into fishery units on other than genetic bases. However, if fishery management units are devised, they should be based on empirically derived exchange rates which should not be confused with true genetic stocks.

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RECENT MARINE STUDIES AT ENEWETAK ATOLL, MARSHALL ISLANDS

John T. Harrison, III

This volume presents contributions of participants at the symposium on recent marine research at Enewetak Atoll, sponsored by the Mid-Pacific Research Laboratory (MPRL) and held at the December 1982 meeting of the Western Society of Naturalists in Long Beach, California. The papers fall into two categories: general research contributions, and specific results of the Enewetak Submersible Program.

As a consequence of their geographic isolation, atolls comprise effective microcosms for the study of processes less approachable in a high island or continental margin ecosystem. Enewetak is the most thoroughly studied atoll in the world. As a former atomic weapons proving ground, Enewetak has provided insight into both short- and long-term environmental responses to radiological contamination. Since the founding of the Enewetak Marine Biological Laboratory (the predecessor of MPRL) in 1954, over a thousand scientists have conducted investigations at Enewetak. Four volumes of collected reprints spanning the period between 1954 and 1979 contain 223 papers which form the foundation of our understanding of atoll ecosystems. The work described in this volume both profits from and augments research conducted at Enewetak over the past four decades.

The contents of the general research papers reflect the diversity which characterizes work performed at Enewetak. Allen et al. discuss the pharmacology of extracts from a wide range of Enewetak marine invertebrates, noting promising anti-cancer potential in 14 natural product concentrates. Boucher and Miller each focus on aspects of dynamic interactions between marine communities. Boucher's nighttime observations of coral predation by muricid gastropod swarms document an alternative mechanism to *Acanthaster*-mediated episodes of reef damage. Using data collected over a 10-year interval, Miller suggests that fluctuations in algal turf density affect physical and biological mortality factors for intertidal invertebrate populations.

Three papers address lagoon sediment environments and the redistribution of properties by bioturbation. Characteristics of bioturbating communities are discussed by Colin et al. and by Suchanek and Colin, while specific influences of *Callianassa* spp. burrowing on radionuclide distribution are presented by McMurtry et al. Additional studies carried out as described in the submersible section underscore the importance of these previously overlooked components of the lagoon ecosystem, particularly in the context of understanding long-term environmental responses to radiological contamination.

Ebert and Ford present results of a 2-year study of spiny lobster populations, concluding that the windward atoll reefs could support a modest fishery producing roughly 1 metric ton (wet weight) per year. These findings are of immediate practical significance to the recently returned native populace of Enewetak which faces the problem of subsistence in a climate of dwindling U.S. foreign aid to Micronesia. The final two papers of this section describe aspects of the behavior of gray reef sharks. Using a wet-submersible, Nelson et al. provoked a series of attacks which were recorded on film and later analyzed for behavioral components in an attempt to better understand the motivation behind attacks on humans by these animals. In a related study, McKibben and Nelson used innovative techniques of ultrasonic telemetry to track gray reef sharks, establishing distinctive patterns of movement and grouping.

The second group of reports presents results of the Enewetak Sumersible Program. During the summer of 1981, 14 scientists from a wide variety of disciplines and home institutions participated in studies of the Enewetak lagoon floor and outer reef slope. The research submersible, MAKALI'I, operated by the Hawaii Undersea Research Laboratory and supported by the National Undersea Research Program of the National Oceanic and Atmospheric Administration, made 52 dives evenly divided between lagoon and outer reef areas. MAKALI'I is a two-man, battery-powered, one-atmosphere submersible with a maximum operating depth of 366 m. During the Enewetak program (which was the submersible's inaugural mission as a research vessel), the equipment inventory included a hydraulic manipulator and cutter; sample storage basket; low-light black and white video camera with internal monitor and VHS recorder; 35-mm still camera and strobe; environmental monitoring package for continuous recording of depth, temperature, salinity, conductivity, oxygen, and incident light; and a directional antenna and pingers. Additional equipment was designed as needed for specific work objectives.

The paper by Colin et al. summarizes the results of the outer reef slope dives and provides the first detailed information on atoll slope geological and biological zonation. Colin also reports on benthic community distribution in the lagoon, using data gathered from submersible and diver observations as well as an extensive benthic remote camera survey. Suchanek et al. draw on both observational and experimental data to point out the environmental significance of callianassid bioturbation in the lagoon floor. The contribution of algae of the genus, *Halimeda,* to the carbonate budget of the atoll is discussed in detail by Hillis-Colinvaux. Although only a fraction of the 106 species of fishes recorded by Randall in his comprehensive survey were observed from the submersible, they comprise important new records for the Marshall Islands. In the final paper, Thresher and Colin describe the Enewetak deep-reef ichthyofauna as observed on numerous submersible dives.

The list of people who have contributed to this effort is too long to allow inclusion of all their names here. Many of them are acknowledged in the individual papers of this volume, but to those whose names are omitted, I extend my apologies and my gratitude. I would particularly like to thank D. Montgomery, P. Helfrich, R. Ray, and K. Grohs for their extra assistance at crucial phases of the project. Support for the Mid-Pacific Research Laboratory was provided by the United States Department of Energy, and additional funding for the Enewetak Submersible Program was provided by the National Oceanic and Atmospheric Administration of the United States Department of Commerce, and by the Defense Nuclear Agency of the United States Department of Defense.

Regrettably, I must end with two somber notes. On 22 September 1983, research operations at the Mid-Pacific Research Laboratory ceased. High level policy decisions resulted in curtailment of funding for the laboratory, and alternative funding could not be secured. Although such events are not uncommon, the uniqueness of the facility and the progress on in-house research efforts as reported in this volume convey special significance to this loss. Fortunately, the laboratory's extensive reference collection was preserved and is presently deposited with the Bernice P. Bishop Museum in Honolulu.

Shortly before the laboratory closed its doors, Dr. D. M. Devaney was lost in a diving accident off Hawaii. As curator of the MPRL reference collection, Dennis was a frequent and welcome visitor to Enewetak. His comprehensive professionalism is reflected in his contributions to this volume, both as a co-author and as a reviewer of preliminary manuscripts. The MPRL family is diminished by his loss, and we dedicate this volume to his abiding memory.

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U.S. Tuna Trade Summary, 1984

SAMUEL F. HERRICK, Jr., and STEVEN J. KOPLIN

Introduction

For much of the U.S. tuna industry, 1984 was a year of frustration and disappointment. As the year ended, the only continental tuna cannery remaining in operation was Pan Pacific Fisheries located at Terminal Island, CA. Two California canneries, Van Camp and Star-Kist, shut down their mainland tuna processing operations in favor of lower cost production at offshore sites, primarily in American Samoa and Puerto Rico. The closure of these canneries left about 2,400 cannery workers without jobs. Businesses that supply the canneries with goods and services and the tuna vessels that traditionally have relied on the canneries located in California to purchase their catches were also severely affected by the closures.

With the tremendous reduction in California canning capacity and a 20-30 percent decline in ex-vessel prices during 1984, vessels participating in the fishery found themselves in a desperate economic situation. Many of the larger, more mobile vessels were able to survive 1984 by operating throughout the Pacific, delivering their catches to offshore sites. Nonetheless, the cannery closures and depressed ex-vessel prices forced a significant number of California-based vessels out of the fishery. By the end of the year the tropical tuna fleet declined by 12 percent. Ten vessels transferred flag, nine were chartered to foreign interests, and three were converted for operation in the North Pacific trawl fisheries.

According to the U.S. tuna industry, foreign competition was the most significant factor contributing to the cannery closures and economic problems of the fleet during 1984. From 1979 through 1984 the amount of canned tuna imported into the U.S. more than tripled (Table 1), increasing by almost 40 percent between 1982 and the end of 1983 alone. This increase has consisted almost entirely of tuna canned in water which has surpassed tuna packed in oil in popularity among U.S. consumers and is subject to a much lower import duty than tuna packed in oil. The problem of canned inports was considered severe enough to prompt various segments of the industry (vessel owners, processors, and cannery workers) to join together and petition the U.S. International Trade Commission (ITC), under Section 201 of the Trade Act of 1974, for

Table 1.—U.S. supply of canned tuna, volume and value, 1974-84.

	Domestic production						
	White[1]		Light[2]		Imports[3]		
Year	Amt.	%[4]	Amt.	%	Amt.	%	Total
Case pack volume (1,000 cases)							
1974	8,162	22.6	25,202	69.9	2,705	7.5	36,069
1975	5,014	17.0	21,788	74.0	2,650	9.0	29,452
1976	5,966	17.9	24,339	73.0	3,020	9.1	33,325
1977	6,221	21.2	21,439	72.8	1,776	6.0	29,436
1978	7,120	18.6	28,515	74.5	2,655	6.9	38,290
1979	5,805	17.0	25,598	74.9	2,754	8.1	34,157
1980	5,505	16.3	25,003	74.0	3,259	9.7	33,767
1981	5,826	16.4	25,928	73.3	3,633	10.3	35,387
1982	6,020	19.1	21,067	66.7	4,491	14.2	31,579
1983	5,127	14.2	24,814	68.5	6,273	17.3	36.214
1984	6,584	16.7	24,461	62.1	8,324	21.1	39,369
Case pack value ($1,000)							
1974	238,518	27.3	585,375	66.9	51,108	5.8	875,001
1975	136,678	19.6	515,957	73.8	45,951	6.6	698,586
1976	212,869	23.1	640,594	69.6	67,502	7.3	920,965
1977	240,734	25.3	665,880	70.0	44,658	4.7	951,272
1978	296,506	22.2	976,754	73.0	63,822	4.8	1,337,082
1979	243,851	20.9	859,998	73.6	65,071	5.5	1,168,920
1980	252,290	20.3	891,237	71.9	97,254	7.8	1,240,781
1981	294,292	22.8	885,846	68.6	110,359	8.6	1,290,497
1982	275,400	26.7	643,046	62.3	113,346	11.0	1,031,792
1983	197,011	19.8	661,586	66.4	137,324	13.8	995,921
1984	255,962	24.6	616,280	59.3	167,268	16.1	1,039,510

[1] Standard case: 48 7-ounce solid pack

[2] Standard case: 48 6.5-ounce chunk pack cans and 48 6-ounce cans of grated flake pack cans.

[3] Standard case: 48 6.5-ounce chunk pack cans.

[4] A % symbol denotes the percent of total for each canned category.

Sources: Domestic: Fisheries of the United States, 1975-84. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv. Curr. Fish. Stat. 6900, 7200, 7500, 7800, 8000, 8100, 8200, 8300, 8320, 8360, var. pagin. and, Canned Fishery Products, 1974-83. Curr. Fish. Stat. 6701, 6901, 7201, 7501, 7801, 8001, 8101, 8201, 8301, 8319, var. pagin. Imports: U.S. Dep Commer., Bur. Census Computerized data files, 1974-84.

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Table 2.—U.S. tuna cannery receipts (short tons) by processing site and direct exports, 1979-84.

Source and species	California-American Samoa-Hawaii							Puerto Rico						
	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$
Domestic														
Albacore	8,518	8,078	14,855	6,965	10,466	10,323	9,776	12	20	2		4	3,565	8
Skipjack	64,641	99,386	83,880	82,669	113,465	94,152	88,808	29,980	15,781	13,950	18,781	41,608	51,441	24,020
Yellowfin	112,349	100,523	100,117	93,468	90,052	59,907	99,302	30,042	18,693	26,049	24,800	30,044	35,193	25,926
Subtotal	185,508	207,987	198,852	183,102	213,983	164,382	197,886	60,034	34,494	40,001	43,581	71,656	90,199	49,954
Imported[2]														
Albacore	36,166	37,664	43,241	33,929	22,750	21,962	34,750	50,773	46,147	44,056	60,670	50,105	70,882	50,350
Skipjack	100,887	103,556	72,189	45,837	50,633	28,737	74,621	87,683	105,075	115,820	82,178	84,675	106,136	95,086
Yellowfin[1]	40,646	36,091	39,293	17,811	14,081	12,685	29,584	33,174	38,382	44,295	33,402	24,251	29,045	34,701
Subtotal	177,699	177,311	154,723	97,577	87,464	63,384	138,955	171,630	189,604	204,171	176,250	159,031	206,063	180,137
Grand total	363,207	385,298	353,575	280,679	301,447	227,766	336,841	231,664	224,098	244,172	219,831	230,687	296,262	230,091

	Direct exports[3]							Total						
	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$
Domestic														
Albacore				62		108	12	8,530	8,098	14,857	7,027	10,470	13,996	9,796
Skipjack	1,961	918	292	387	45	14,385	721	96,582	116,085	98,122	101,837	155,118	159,978	113,549
Yellowfin[1]	3,945	1,339	1,087	3,864	538	15,077	2,155	146,336	120,555	127,253	122,132	120,634	110,177	127,383
Subtotal	5,906	2,257	1,379	4,313	583	29,570	2,888	251,448	244,738	240,232	230,996	286,222	284,151	250,728
Imported[2]														
Albacore								86,939	83,811	87,297	94,599	72,855	92,844	85,100
Skipjack								188,570	208,631	188,009	128,015	135,308	134,873	169,707
Yellowfin[1]								73,820	74,473	83,588	51,213	38,332	41,730	64,285
Subtotal								349,329	366,915	358,894	273,827	246,495	269,447	319,092
Grand total	5,906	2,257	1,379	4,313	583	29,570	2,888	600,777	611,653	599,126	504,823	532,717	553,598	569,820

[1] Includes bigeye, blackfin, and bluefin tuna.
[2] Includes only imported tuna destined for canning; exludes tuna imported as flakes, tuna not fit for human consumption, and "sushi" grade tuna.
[3] Includes tuna landed directly or transshipped to a foreign country; excludes tuna exported from the east coast.
Source: Industry Analysis and Information Section, Southwest Region, NMFS, NOAA.

tariff relief from imports of canned tuna packed in water [Int. Trade Comm. Docket No. 1034, 1984].

Although the ITC acknowledged that the tuna industry was facing difficult times, the Commission decided that the substantial increases in imports of relatively low-cost tuna canned in water, while a contributing factor, was not the primary cause of the industry's current economic plight. Rather, the majority of Commissioners found that overinvestment in boats, plants, and inventories during a period of exceptionally high interest rates was just as important, if not more so, in bringing about the industry's present economic condition (ITC, 1984). This finding thwarted industry's bid for tariff relief to limit the flow of canned tuna imports. A subsequent attempt by the industry to have the U.S. Congress enact protective tariff legislation also failed.

With the cannery and vessel dislocations that occurred during 1984, domestic cannery receipts[1] of imported and domestically caught albacore, *Thunnus alalunga* (white meat), and tropical (light meat) tunas (skipjack, *Euthynnus pelamis*; yellowfin, *Thunnus albacares*; blackfin, *T. atlanticus*; bluefin, *T. thynnus*; and bigeye tuna, *T. obesus*) were slightly below those for 1983. The total volume was 524,028 short tons (t), a decrease of less than 2 percent) from the total volume for 1983 and 8 percent below the 1979-1983 average volume of annual cannery receipts (Table 2). Domestically caught cannery deliveries amounted to 254,581 tons, 11 percent below the 1983 level but 3 percent above the 1979-83 average. Imports made up the 269,447-ton balance in total cannery supplies for 1984, a 9 percent increase in raw tuna imports from 1983 imports but 16 percent below the 1979-83 average.

A significant occurrence in 1984 was the increase in deliveries and transshipments of U.S.-caught tropical tuna to foreign canneries. The U.S. fleet landed 29,570 tons of tuna for export, most of which was transshipped to canneries in Thailand, Japan, and Italy. This compares to only 583 tons exported in 1983 and a 1979-83 annual average of 2,888 tons. When exports of domestically caught raw tuna are combined with deliveries of domestically caught tuna to U.S. canneries, total U.S. deliveries amounted to 284,151 tons for 1984, less than 1 percent below the corresponding amount for 1983 (Table 2). The surge in U.S. exports is an indication of the internationalization of tuna trade in general and, more specifically, a possibly increasing reliance of U.S. vessels on foreign markets.

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[1] Cannery receipts include only tuna destined for U.S. canneries. Cannery receipts exclude U.S.-caught tuna landed at foreign sites, U.S.-caught tuna landed at U.S. sites that is destined for foreign canneries, U.S.-caught tuna destined for the fresh-fish market, tuna imported as flakes, imported tuna not fit for human consumption, and imported "sushi" grade tuna.

The western Pacific Ocean[2] continued to be the most productive tuna fishing area during 1984, accounting for 188,000 tons or 66 percent of the total receipts of domestically caught raw tuna and U.S. exports of raw tuna by oceanic area. This represents a 10 percent increase from 1983 and is three times the 1979-83 average volume of annual cannery receipts of domestically caught tuna and raw tuna exports from this area.

Despite the loss in U.S. west coast processing capacity and intense competition from foreign producers, overall U.S. canned tuna production in 1984 rose 4 percent from 1983. Total volume was 31.0 million standard cases[3], 3 percent above the 1979-83 average total annual volume. When canned imports were combined with U.S. production, the total addition to U.S. canned supplies was 39.4 million standard cases for 1984 which was 8 percent above 1983 and 15 percent above the 1979-83 average annual additions to canned supplies (Table 1).

Increased competition between foreign and domesticaly produced canned tuna has been beneficial to U.S. consumers. The retail composite canned tuna price, which decreased nearly 7 percent during 1983, fell an additional 3 percent in 1984. The downward price trend contributed to corresponding growth in overall apparent consumption which increased 2 percent in 1984, following an increase of 7 percent for 1983. Water-packed products led sales in all categories during 1984, with a gain of almost 10 percent from 1983. Since these items account for more than 60 percent of total sales, this increase helped offset reduced sales of light tuna in oil and of health-oriented, canned tuna products.

In the following sections, the 1984 production of white and light meat tuna by the U.S. tuna industry and consumption of tuna products by U.S. consumers is reviewed in more detail. In the final section some of the issues and events that affected the industry's performance in 1984 are analyzed. Unless otherwise noted, the information and data presented were compiled by the Industry Analysis and Information Section of the Southwest Region, National Marine Fisheries Service, NOAA.

U.S. Albacore Production

Albacore, which in the United States is the only species that may be labelled as white meat tuna (USFDA, 1985), showed all-around trade improvement in 1984. According to industry reports, consumption of canned white meat tuna increased nearly 1 percent for oil pack and 6 percent for water pack during 1984. Total cannery receipts (domestically caught albacore plus imports) reached 106,732 tons in 1984, 28 percent above receipts for 1983 and the highest they have been in the past 5 years (Table 2). Domestic white meat production for 1984 amounted to 6.6 million standard cases, 28 percent ahead of 1983 production and 16 percent greater than the 1979-83 average. The substantial gains in cannery deliveries and domestic production in 1984 probably reflected the industry's expectations of continued growth in consumption, which had increased substantially during 1983.

The U.S. albacore fishery presently occurs entirely in the Pacific Ocean north of lat. 25°N and off the west coast to about long. 180°. This area is divided at long. 140°W into offshore (mid-Pacific) and inshore fishing areas.

Cannery Receipts of Domestically Caught Albacore

With relatively tight supplies of albacore worldwide putting upward pressure on ex-vessel prices and with favorable environmental conditions following the 1982-83 El Niño episode, prospects for the 1984 U.S. albacore fishery appeared to be a continuation of the upswing which began in 1983 (Squire, 1983). Only the announcement by Hawaiian Tuna Packers that it would not buy albacore at its Honolulu plant dimmed this outlook. However, Hawaiian Tuna Packers later retracted and agreed to purchase 400 tons of albacore from fishermen who had delivered to the cannery in the past. The uncertainty surrounding purchases of albacore by Hawaiian Tuna Packers deterred a large number of U.S. vessels from fishing in the mid-Pacific area early in 1984. About 30-40 vessels fished in the mid-Pacific during 1984, down 45 percent from 1983, and cannery deliveries from this area were 18 percent below those for 1983.

The albacore catch in the inshore areas (east of long. 140°W) increased 19 percent above that for 1983. A significant occurrence in 1984 was the unusually large catch of albacore by purse seiners: 4,100 tons were caught 50-100 miles off San Diego, Calif., during July and August (Majors and Miller[4]). Not since the early 1960's have purse seiners contributed to annual landings of North Pacific albacore in this magnitude. Troll gear (jig boats) is the dominant gear in the U.S. fishery.

Deliveries of domestically caught albacore to U.S. canneries totaled 13,888 tons in 1984, up 32 percent from 1983 and 42 percent above the 1979-83 average. This significant increase in receipts of domestically caught albacore can be largely attributed to highly propitious economic and environmental conditions. In addition, 108 tons of U.S.-caught albacore were exported in 1984, whereas no albacore was exported in 1983 (Table 2).

With production decreasing 15 percent and consumption increasing 17 percent during 1983, the U.S. white meat tuna supply entering 1984 was at a relatively low level. Consequently, fishermen were able to negotiate an early season ex-vessel contract price of $1,400 per ton for albacore ≥9 pounds, and $1,125 per ton for fish <9 pounds, increases of 12 and 15 percent, respectively, over the 1983 prices. Accompanying the increase in ex-vessel prices was a

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[2] In this paper, the eastern and western Pacific are distinguished at long. 150°W.

[3] A standard case can consist of: Solid 48 (7-ounce) = 21 pounds; Chunk 48 (6.5-ounce) = 19.5 pounds; Grated/Flake 48 (6-ounce) = 18 pounds.

[4] Majors, A. P., and F. Miller. 1985. Summary of the 1984 North Pacific albacore fishery data. NMFS Southwest Fish. Cent., La Jolla, Calif. SWFC Admin. Rep. LJ-85-14, 14 p.

Table 3.—U.S. cannery ex-vessel (contract) prices (dollars per short ton) at California and Puerto Rico, 1979-84.

	Albacore			Skipjack tuna				Yellowfin tuna				
Year	>18 lbs.	9-18 lbs.	<9 lbs.	>7.5 lbs.	4-7.5 lbs.	3-4 lbs.	<3 lbs.	Greater than 20 lbs.	7.5-20 lbs.	4-7.5 lbs.	3-4 lbs.	<3 lbs.
1979				$740-790	$740-790	$590	$400	$840	$840	$700-790	$700-790	$700-790
	$1,390	$1,320	$1,320	740-760	740-760	590-610	400-420	850-860	850-860	700-720	700-720	700-720
				760-805	760-805	610-655	420-505	860-905	860-905	720-765	720-765	720-765
	1,390	1,390	1,390	805-850	805-850	655-700	505-545	905-950	905-950	765-810	765-810	765-810
				850	850	700	545	950	950	810	810	810
1980	1,610	1,610	1,610	850	850	700	545	950	950	810	810	810
	1,635	1,635	1,635	1,100	1,100	1,000	800	1,200	1,200	1,100	1,100	1,100
1981	1,800	1,800	1,800	1,100	1,100	1,000	800	1,200	1,200	1,100	1,100	1,100
1982	1,425	1,425	1,425	1,100	1,100	1,000	800	1,200	1,200	1,100	1,100	1,100
				1,040	1,040	940	740	1,140	1,140	1,040	1,040	1,040
	1,350	1,225	1,000	890	890	700	500	1,170	1,050	890	890	890
1983[1]				950	850	700	420	1,230	1,050	850	700	420
	1,250	1,250	975	900	800	640	420	1,125	990	800	640	400
				880	780	585	250	1,125	975	780	585	250
1984[1]	1,400	1,400	1,125	830	730	500	250	1,085	950	730	500	250
				850	750	550	250	1,000	900	750	550	250
	1,150-1,300	1,150-1,300	875-1,025	763	650	470	235	925	800	650	470	235

[1] Skipjack and yellowfin prices are for standard grade, prices may vary due to quality.
Source: Industry Analysis and Information Section, Southwest Region, NMFS, NOAA.

return to normal water temperatures, well developed temperature fronts, and good upwelling. These conditions were highly conducive to albacore fishing as evidenced by the exceptional purse seine catches from the inshore areas early in the season (Majors and Miller[4]).

However, by mid-season, following the unprecedented purse seine catches, ex-vessel prices dipped to $1,150 per ton for large fish and $875 per ton for small fish. Prices recovered somewhat after the influx of purse seine caught albacore, closing the season at $1,300 per ton for large fish and $1,025 per ton for small fish, still 4 and 5 percent, respectively, ahead of 1983 prices (Table 3).

Cannery receipts from the 1984 fishery generated more than $17 million in ex-vessel revenue, up 31 percent from 1983. Dividing 1984 ex-vessel albacore revenue by total U.S. cannery deliveries yields a weighted ex-vessel price of $1,252 per ton, down 1 percent from 1983, the lowest it has been in the past five years (Table 4).

Table 4.—U.S. cannery ex-vessel (weighted) prices (dollars per short ton), 1979-84.

	Albacore		Skipjack tuna		Yellowfin tuna	
Year	Nominal	Real[1]	Nominal	Real[1]	Nominal	Real[1]
1979	1,286	787	728	445	863	528
1980	1,659	930	1,063	596	1,180	661
1981	1,800	920	1,030	527	1,170	598
1982	1,387	669	965	465	1,123	542
1983	1,268	589	799	371	1,032	479
1984	1,252	560	760	340	982	440

[1] Adjusted for inflation using GNP implicit price deflator (1972 = 100).
Source: Industry Analysis and Information Section, Southwest Region, NMFS, NOAA.

Canned Albacore Production

At the beginning of 1984, the major U.S. tuna receiving and processing sites were San Diego and Terminal Island, Calif., Mayaguez and Ponce, Puerto Rico; Honolulu, Hawaii; and Pago Pago, American Samoa. With the closure of the Van Camp cannery in San Diego in mid-1984, which left only two California canneries in operation, tuna receipts and production data could no longer be reported separately for California without violating confidentiality requirements. Hence, California receipts and production data were combined with those from American Samoa and Hawaii (ASCH) for reporting purposes. Similar data for Puerto Rico are reported separately.

Of the total amount of raw (whole and other than whole) albacore supplied to canneries in 1984 (106,732 tons), 70 percent was delivered to canneries in Puerto Rico and the balance to canneries in ASCH. This resulted in a 49 percent increase from 1983 in albacore deliveries to Puerto Rico and a 2 percent decline in deliveries to ASCH. Seventy-five percent of the 1984 domestically caught albacore, or 10,323 tons, was received by ASCH canneries and the remainder, 3,565 tons, was transshipped to canneries in Puerto Rico from west coast ports (Table 2). This is a 1 percent decrease from 1983 in domestically caught albacore deliveries to ASCH. In 1983, only 4 tons of domestically caught albacore were received in Puerto Rico.

U.S. canneries received 92,844 tons of imported raw albacore in 1984, up 27 percent from 1983 (Table 2). Imports made up 87 percent of the total 1984 cannery supply of albacore, the same as in 1983. Puerto Rico was the major receiving site for imports with 70,882 tons or 76 percent of total albacore imports. ASCH received the rest. Albacore imports received in Puerto Rico during 1984 increased 41 percent from 1983, while imports received in ASCH decreased 3 percent. The leading exporter of raw albacore to U.S. canneries in 1984 was the Canary Islands,

Table 5.—Cannery imports of frozen tuna (short tons) by country of origin, 1979-84.

Source[1]	1979		1980		1981		1982		1983		1984	
	White	Light[2]	White	Light	White	Light	White	Light	White	Light	White	Light
Brazil		1,002	109	5,847	83	5,968	1,443	16,181	1,185	15,154	2,018	7,743
Canary Island	1,939	1,116	362		325		1,693	1	7,653	5	14,030	10
Cayman Island						2,171		6,723				9,960
Eduador		16,132	340	10,661						2,809		12,034
Ghana	215	41,102	70	30,071	760	36,188	1,078	27,783	345	23,751	170	6,640
Ivory Coast	162	10,141		12,860	345	35,805		27,862		13,783	289	30,997
Japan	7,310	10,694	3,957	45,112	6,483	12,307	5,834	12,705	696	18,426	10,946	20,965
Mauritius	6,038		4,349		1,364	152	4,811		4,668		5,026	
Netherlands Antilles	5,737	3,984	6,611	4,869	6,202	273	10,054	1,996	8,560	258	9,619	298
Panama		32,460		27,660		23,746		29,558	1	8,110	424	13,928
Philippines	60	27,210	37	26,799		20,781		5,923		6,476		1,327
Reunion	7,118	79	9,209	157	4,738	204	12,036	146	7,438	3	4,363	67
Seychelles										3,042		8,257
Singapore	3,613	1,505	3,444	5,366	3,969	7,781	1,386	3,846	4,217	3,761	5,024	
Solomon Island		17,328	1,088	18,984		22,618		928		10,600		15,836
South Africa	13,818	75	14,136	263	15,091	1,832	17,044	1	7,304	239	11,856	1,478
South Korea	372	485	412	925	1,547	4,893	1,001	6,891	5,374	13,830	2,119	11,064
Taiwan	983	34		244	1,730	169	99	384	5,075	3,851	9,739	9,468
Uruguay	9,988	48	7,903	1,719	9,920	1,489	8,835	670	4,480	143	3,228	722
Venezuela	222	1,153		865	394	5,496		2,421	1	6,604		7,002
Other	29,364	97,842	31,784	90,702	34,346	89,724	29,285	35,209	15,858	42,795	13,993	18,807
Total	86,939	262,390	83,811	283,104	87,297	271,597	94,599	179,228	72,855	173,640	92,844	176,603

[1] Data reflects the origin of shipments and not necessarily the flag of the catcher vessel.
[2] Light meat includes bigeye, blackfin, bluefin, skipjack, and yellowfin tuna.
Source: Industry Analysis and Information Section, Southwest Region, NMFS, NOAA.

Spain[5], with 14,030 tons or 15 percent of the total imports. South Africa was next with 11,856 tons, 12 percent of the total (Table 5).

Raw albacore imports received at U.S. canneries in 1984 were valued at about $145 million, up 42 percent from 1983. Dividing this value by the corresponding volume results in a weighted average import price of $1,561 per ton for raw albacore in 1984, nearly 17 percent above that for 1983.

The Pacific Ocean provided 44 percent of the total cannery supply of raw albacore in 1984. The Atlantic and Indian Oceans followed with 42 percent and 14 percent, respectively, of the total supply, all imports. The supply of albacore from the Pacific Ocean, 46,775 tons, represented a 37 percent increase from 1983, and that from the Atlantic, 44,601 tons, was a 34 percent increase from 1983. The Indian Ocean was the only oceanic area for which a decrease in supply (11 percent) occurred in 1984 (Tables 6 and 7).

White meat tuna production in Puerto Rico amounted to 4.6 million standard cases in 1984, 70 percent of the total U.S. albacore pack, and a 35 percent increase from 1983. ASCH produced 2.0 million standard cases of white meat tuna in 1984, down 18 percent from 1983.

Wholesale list prices for U.S.-produced, nationally advertised brands of white meat tuna remained between $55.50 and $60.15 per standard case throughout 1984. With discounts, the actual selling price at wholesale was as low as $42.25 for a standard case, a 12 percent increase over 1983. Production of both nationally advertised and private label (advertised and private brands) white meat tuna was valued at $256 million in 1984, up 30 percent from 1983. Based on total white meat volume, the weighted average value of unit production during 1984 was $38.88 per standard case compared with $38.43 in 1983, a 4 percent increase.

Tropical Tuna Production

Although U.S. consumption of tropical or light meat tuna products increased during 1984, corresponding processing showed a slight decline. Consumption of canned, light meat tuna packed in water increased nearly 9 percent, and consumption of oil-packed, light meat tuna decreased 6 percent. This led to an overall increase in light meat consumption of approximately 3 percent in 1984, based on relative market shares. Cannery production of all light meat products totaled 24.5 million standard cases in 1984, a decrease of 1 percent from 1983 and from the 1979-83 average (Table 1). The total cannery supply of light meat tuna, 417,296 tons, also declined 1 percent from 1983 and was 7 percent below the 1979-83 average (Table 2). Prices at the ex-vessel, wholesale, and retail levels continued to decline during 1984.

Domestically Caught Tropical Tuna Cannery Receipts

The U.S.-flag tropical or light meat tuna fleet consisted of 145 vessels at the start of 1984: 125 purse seiners and 20 baitboats (pole-and-line gear). By the end of 1984, the fleet had declined to 130 vessels: 109 purse seiners and 21 baitboats, with a total carrying capacity of 113,269 tons, a 12 percent decrease from 1983. However, 29 of these vessels were listed as inactive, and 18 of the vessels were seiners of individual carrying capacities of 400 tons or more.

The fleet operated almost exclusive-

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[5] The exporting country reflects origin of shipments and not necessarily the flag of the catcher vessel.

Table 6.—U.S. domestic tuna cannery receipts and direct exports[1] (short tons) by ocean of origin, 1979-84 (None from Indian Ocean).

	Albacore							Skipjack tuna						
Ocean	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$
E. Atlantic	12	2	2	62			16	1,384	2,458	3,327	27	21		1,444
W. Atlantic		18	4		4		5	501	25	108		3	233	127
E. Pacific	6,914	7,690	13,954	5,099	9,434	13,409	8,618	83,944	101,344	74,116	59,264	40,181	22,067	71,770
W. Pacific	1,604	388	897	1,866	1,032	587	1,157	10,753	12,258	20,571	42,546	114,913	137,678	40,208
Subtotal	8,530	8,098	14,857	7,027	10,470	13,996	9,796	96,582	116,085	98,122	101,837	155,118	159,978	113,549

	Yellowfin tuna[2]							Total						
	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$
E. Atlantic	2,396	1,898	1,966	1,087			1,470	3,792	4,358	5,295	1,176	21		2,930
W. Atlantic	615	517	502	115	70	577	364	1,116	560	614	115	77	810	496
E. Pacific	142,667	116,947	110,251	96,640	65,863	59,823	106,474	233,525	225,981	198,321	161,003	115,478	95,299	186,862
W. Pacific	658	1,193	14,534	24,290	54,701	49,777	19,075	13,015	13,839	36,002	68,702	170,646	188,042	60,440
Subtotal	146,336	120,555	127,253	122,132	120,634	110,177	127,383	251,448	244,738	240,232	230,996	286,222	284,151	250,728

[1] Includes tuna landed directly or transshipped to a foreign country; excludes tuna exported from the east coast.
[2] Includes bigeye, blackfin, and bluefin tuna.
Source: Industry Analysis and Information Section, Southwest Region, NMFS, NOAA.

Table 7.—U.S. imported tuna cannery receipts[1] (short tons) by ocean of origin, 1979-84.

	Albacore							Skipjack tuna						
Ocean	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$
E. Atlantic	16,843	14,567	17,105	19,815	16,935	27,392	17,053	50,218	40,318	67,011	49,417	34,358	35,882	48,265
W. Atlantic	20,352	15,016	16,894	21,129	16,127	17,209	17,904	3,211	6,546	8,754	17,119	18,070	9,059	10,740
E. Pacific	20	418	22	48	243	439	150	40,015	23,981	9,409	11,916	4,501	9,245	17,964
W. Pacific	32,955	36,808	43,638	35,375	23,226	32,340	34,400	93,837	132,283	95,119	44,017	72,742	72,699	87,600
Indian	16,769	17,002	9,638	18,232	16,324	15,464	15,593	1,289	5,503	7,716	5,546	5,637	7,988	5,138
Subtotal	86,939	83,811	87,297	94,599	72,855	92,844	85,100	188,570	208,631	188,009	128,015	135,308	134,873	169,707

	Yellowfin tuna[2]							Total						
	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$	1979	1980	1981	1982	1983	1984	79-83 $\bar{x}$
E. Atlantic	6,588	6,589	19,561	9,320	4,618	3,258	9,335	73,649	61,474	103,677	78,552	55,911	66,532	74,653
W. Atlantic	2,119	2,194	5,200	3,058	6,446	3,259	3,803	25,682	23,756	30,838	41,306	40,644	29,527	32,447
E. Pacific	39,637	30,891	16,039	19,200	7,492	9,222	22,652	79,672	55,290	25,470	31,164	12,236	18,906	40,766
W. Pacific	24,997	34,060	41,340	18,800	18,814	23,799	27,602	151,789	203,151	180,097	98,192	114,781	128,838	149,602
Indian	479	739	1,448	835	962	2,192	893	18,537	23,244	18,802	24,613	22,923	25,644	21,624
Subtotal	73,820	74,473	83,588	51,213	38,332	41,730	64,285	349,329	366,915	358,894	273,827	246,495	269,447	319,092

[1] Includes only imported tuna destined for canning; excludes tuna imported as flakes, tuna not fit for human consumption, and ''sushi'' grade tuna.
[2] Includes bigeye, blackfin, and bluefin tuna.
Source: Industry Analysis and Information Section, Southwest Region, NMFS, NOAA.

ly in the Pacific Ocean during 1984. Vessels active in the western Pacific numbered 61 at the beginning of 1984, with a combined carrying capacity of 72,562 tons. The number in the western Pacific declined to 43 at the end of 1984 with a capacity of 52,245 tons, a 28 percent decrease in both number and total capacity. Thirty-seven vessels, with a total carrying capacity of 25,150 tons, operated in the eastern Pacific during the first quarter of 1984 increasing to 58 vessels with a capacity of 39,623 tons by the end of the year, an increase of 57 percent in both number of vessels and capacity. Only four U.S.-flag vessels, having a combined capacity of 4,780 tons, fished in the Caribbean area of the Atlantic Ocean during 1984.

Cannery receipts of domestically caught, light meat tuna totaled 240,693 tons in 1984, 13 percent below 1983. This total comprised 145,593 tons of skipjack tuna and 95,100 tons of yellowfin tuna (includes bigeye, bluefin, and blackfin tuna), decreases from 1983 of 6 percent and 21 percent, respectively. In addition to deliveries to U.S. canneries, the U.S.-flag vessels exported 29,462 tons to foreign canneries, compared with 583 tons in 1983. Total exports consisted of 14,385 tons of skipjack and 15,077 tons of yellowfin tuna (Table 2).

Ex-vessel prices for light meat which declined in 1983, fell further in 1984 (Table 3). The contract ex-vessel price (without quality adjustments[6]) for skipjack tuna in the 3- to 4-pound range was $470 per ton at the end of 1984, 20 percent below that at the close of 1983. The contract ex-vessel price for yellowfin tuna in the 7.5- to 20-pound range (without quality adjustments[6]) at the end of 1984 was $800 per ton, 18 percent below the corresponding price at the end of 1983. The reported ex-vessel value of domestically caught skipjack tuna receipts was $110 million in 1984, an 11 percent decrease from 1983. This yields a weighted ex-vessel price of $760 per ton, down 5 percent from 1983 (Table 4). Domestic deliveries of yellowfin tuna generated about $93 million in ex-vessel revenue for 1984, 25 percent below 1983. The weighted ex-vessel price for yellowfin tuna in 1984 was $982 per ton, also down 5 percent from 1983 (Table 4). Total ex-vessel revenue was about $203 million in 1984, an 18 percent decrease from 1983.

Canned Tropical Tuna Production

Skipjack, yellowfin, bigeye, and bluefin tunas are canned as light meat in the United States. The 6.5-ounce can of chunk style, light meat tuna in water was the most popular tuna product consumed in the United States during 1984, accounting for over 45 percent of all tuna sales.

The total supply of raw, light meat tuna, 417,296 tons, was delivered to canneries in Puerto Rico, American Samoa, Hawaii, and California during 1984. Puerto Rico was the leading receiving site in 1984 with 221,815 tons, 53 percent of the total U.S. cannery supply. The balance, 195,481 tons, was received at canneries in ASCH. Total receipts for Puerto Rico increased 23 percent from 1983, and decreased 27 percent for ASCH (Table 2). This reflects the diversion of deliveries to Puerto Rico due to the cannery closures in California.

Of the total receipts of domestically caught light meat tuna for 1984, 154,059 tons (64 percent) were received in ASCH, and the remainder, 86,634 tons, went to Puerto Rico. Again, the cannery closures on the U.S. west coast were a major factor contributing to the 25 percent decrease from 1983 in deliveries of domestically caught, light meat tuna to ASCH, and the 21 percent increase in deliveries to Puerto Rico (Table 2).

Light meat imports totaled 176,603 tons in 1984, almost 2 percent ahead of 1983. Imports made up 42 percent of the total cannery supply in 1984 versus 39 percent in 1983. Puerto Rico was the major receiving site for imports during 1984 with 135,181 tons (77 percent of the total), a 24 percent increase from 1983 (Table 2).

Skipjack tuna dominated imports in 1984 with 134,873 tons making up 76 percent of the total imports. Yellowfin tuna contributed the balance. Overall, skipjack tuna imports were down less than 1 percent from 1983, while yellowfin imports increased 9 percent (Table 2).

The top exporter of raw light meat tuna to the United States in 1984 was the Ivory Coast, with 30,997 tons or 18 percent of the 1984 total. Japan followed with 20,965 tons, 12 percent of the total (Table 5).

The total value of imports received at U.S. canneries in 1984 was $137 million, down less than 1 percent from 1983. The value of skipjack tuna imports was about $95 million, and the value of yellowfin tuna imports was about $42 million, a decrease from 1983 of 5 percent for skipjack tuna and an increase of 4 percent for yellowfin tuna. These values convert to weighted average prices of $704 per ton for imported skipjack tuna and $1,009 per ton for imported yellowfin tuna, a decrease from 1983 of 5 percent and an increase of 3 percent, respectively.

The Pacific Ocean was the primary source of all (domestically caught plus imports) U.S. cannery receipts of light meat tuna and domestically caught, light meat tuna exports to foreign canneries which together totaled 446,758 tons in 1984. The Pacific provided 384,300 tons or 86 percent of this total, the Atlantic Ocean 12 percent, and the Indian Ocean 2 percent, virtually all imports. On a regional basis, the western Pacific was the leading production area with 283,953 tons, 64 percent of total receipts and exports, an increase of 8 percent from 1983. Of the total receipts originating in the western Pacific during 1984, 66 percent (187,455 tons which includes U.S. exports) was domestically caught, and the remainder (96,498 tons) consisted of imports. Skipjack tuna was the predominant species in the western Pacific receipts and U.S. exports. Other oceanic regions contributing to the 1984 U.S. cannery supply and U.S. raw exports, in order of importance, were the eastern Pacific (primarily domestically caught yellowfin tuna), the eastern Atlantic (almost all skipjack tuna imports), and the western Atlantic (mainly skipjack tuna imports). A breakdown of the 1984 cannery supply and U.S. exports by ocean of origin is given in Tables 6 and 7.

Puerto Rico was the leading U.S. processing center for canned light meat tuna during 1984 with 12.6 million standard cases, 52 percent of the total light meat pack for 1984. This is an increase of 26 percent from 1983. The remaining 11.8 million standard cases were processed at canneries in ASCH, which is a decrease of 7 percent from 1983.

The wholesale list price of U.S.-produced, advertised, light meat tuna remained steady at between $40.05 and $40.64 per standard case, but it was discounted to $36.00 per standard case at the beginning of 1984 and declined to $32.00 by the end of the year, an 11 percent decrease. Total production of canned light meat tuna in 1984, both advertised and private label brands, was valued at $616 million, down 7 percent from 1983. Dividing total value by total volume yields a weighted average unit production price of $25.91 for a standard case of light meat tuna in 1984, 6 percent below that for 1983.

Canned Tuna Imports

The U.S. tariff on imports of canned tuna packed in oil is different from that on imports of canned tuna not packed in oil. Tuna in oil is subject to a 35 percent tariff; thus, imports are negligible. Canned tuna not in oil is under a tariff rate quota which allows imports up to 20 percent of the previous year's domestic production, excluding production at American Samoa, to enter at 6 percent ad valorem, and imports above the quota level enter at 12.5 percent ad valorem. Before the quota on canned imports not in oil is reached, the Bureau of the Census reports statistics on white meat and light meat imports separately. However, once the quota is reached Bureau of the Census records are combined for white and light meat imports so that a distinction between the two no longer exists. Therefore, year-end figures represent imports of both canned light and white meat not in oil.

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[6] Contract prices may be adjusted for salt content, unloading temperature, and condition of the fish.

The 1984 quota on canned imports not in oil was 95,587,400 pounds or about 4.9 million standard cases. Total imports reached a record 162.3 million pounds or 8.3 million standard cases, an increase of 33 percent from 1983. When the 1984 quota was initially reached on 16 July, white meat made up 13 percent of the imports of canned tuna not in oil. Imports of canned tuna in oil, practically all light meat tuna, totaled 277,000 pounds or about 14,000 standard cases, an increase of 40 percent from 1983.

Thailand exported the most canned tuna to the U.S. in 1984—89.7 million pounds or 4.6 million standard cases. This was 55 percent of the total and represents a 127 percent increase in imports of canned tuna from Thailand over 1983. Japan was a distant second with 26.9 million pounds or 1.4 million standard cases, 17 percent of the 1984 total.

Imports in 1984 were valued at about $167 million free on board, an increase of 22 percent from 1983. This converts to a weighted average price of $1.03 per pound or $20.09 per standard case which is 8 percent below that for 1983. Imports of canned tuna and their corresponding value by major exporting country are shown in Table 8.

Table 8.—U.S. imports for consumption by principal sources tuna in airtight containers (oil and water), 1979-1984.

Source	1979	1980	1981	1982	1983	1984
Quantity (1,000 pounds)						
Japan	28,366	24,794	21,271	26,481	20,387	26,855
Philippines	6,998	13,777	21,451	27,631	32,018	22,225
Thailand	4,844	6,405	10,315	18,667	39,930	89,685
Taiwan	12,282	15,947	15,771	10,704	18,710	17,935
Australia			58	1,930	2,799	
Malaysia	292	66	696	755	3,083	1,608
Indonesia			146	595	2,634	2,222
Maldives	62	600	592	327		
Spain[1]	336	146	170	120	133	214
Singapore		28	65	120	329	58
Other	523	1,792	316	248	2,306	1,511
Total	53,704	63,553	70,852	87,579	122,329	162,313
Value ($1,000)						
Japan	37,055	42,015	36,453	38,561	24,643	29,186
Philippines	7,319	20,043	30,504	31,085	32,291	20,396
Thailand	5,135	8,875	15,400	22,711	43,259	89,253
Taiwan	14,103	23,316	24,631	14,366	22,772	22,475
Australia			105	3,451	3,684	
Malaysia	314	76	1,230	1,242	4,068	1,893
Indonesia			209	699	2,679	2,102
Maldives	67	825	874	379		
Spain[1]	501	367	402	300	268	376
Singapore		38	91	141	386	44
Other	579	1,698	459	412	3,274	1,545
Total	65,071	97,254	110,358	113,347	137,324	167,270
Unit value ($ per pound)						
Japan	$1.31	$1.69	$1.71	$1.46	$1.20	$1.09
Philippines	1.05	1.45	1.42	1.12	1.00	0.92
Thailand	1.06	1.39	1.49	1.22	1.08	1.00
Taiwan	1.15	1.46	1.56	1.34	1.21	1.26
Australia			1.80	1.79	1.31	
Malaysia	1.08	1.14	1.77	1.64	1.31	1.18
Indonesia			1.43	1.18	1.01	0.95
Maldives	1.07	1.38	1.48	1.16		
Spain[1]	1.49	2.52	2.36	2.50	2.01	1.76
Singapore		1.38	1.41	1.17	1.17	0.76
Other	1.11	0.95	1.45	1.66	1.41	1.03
Average	1.21	1.53	1.56	1.29	1.12	1.03
Percentage of total quantity						
Japan	53	39	30	30	17	17
Philippines	13	22	30	32	26	15
Thailand	9	10	15	21	33	55
Taiwan	23	25	22	12	15	11
Australia			*[2]	2	2	
Malaysia	*	*	1	1	2	1
Indonesia			*	1	2	1
Maldives	*	1	1	*		
Spain[1]	1	*	*	*	*	*
Singapore		*	*	*	*	*
Other	1	3	1	1	3	1
Total	100	100	100	100	100	100

[1] Mainly oil packed.
[2] An asterisk means less than 1 percent, included in "Other" listing.
Source: Department of Commerce, Bureau of the Census computerized data files, 1979-84.

U.S. Consumption of Canned Tuna

Per capita U.S. consumption of canned tuna products for 1984 (excluding consumption by military personnel) was estimated at 3.2 pounds, 3 percent above 1983. If it is assumed that during 1984 canned light and canned white meat tuna were consumed in the same proportions that they were produced in the U.S. (21 percent white meat, 79 percent light meat), per capita domestic consumption would be about 0.67 pounds of white meat tuna and 2.53 pounds of light meat tuna. This converts to 1.5 standard cans of white meat tuna and 6.2 standard cans of light meat tuna per capita. Compared with 1983, per capita consumption of white meat tuna increased 24 percent in 1984 and increased 3 percent for light meat tuna. Based on the National Marine Fisheries Service's "Operation Price Watch" (USDOC, 1983, 1984), which monitors the average price for domestically produced canned tuna in 10 U.S. cities, consumers paid an average of $1.47 per can for white meat tuna and $.86 per can for light meat tuna during 1984 (although retail promotions sometimes reduced light meat prices to $.59 per can), a decrease of 1 percent for both white and light meat from 1983. This results in a slight increase in estimated per capita expenditures on canned tuna in 1984—$7.54 versus $7.10 in 1983. These estimates are based on U.S. canned production and retail price information and do not take into account domestic consumption of imported canned tuna.

Discussion

Industry performance during 1984 was characterized by increased receipts of domestically caught albacore tuna, only a slight decrease in domestically caught tropical tuna destined for U.S. and foreign canneries, an increase in total domestic canned production, and continued growth in U.S. consumption of canned tuna products. This showing, however, offered little consolation to unemployed California cannery workers, purse seine crewmen, and vessel operators who lost their jobs when all but one major processor left the U.S. west coast.

Perhaps the most significant event affecting the U.S. tuna industry, or at least that which dominated the public's attention, was the industry's petition for a more equitable tariff on imports of canned tuna not in oil (in water) submitted to the International Trade Commission in early 1984. Citing rapid and substantial increases in import penetration that threatened to bring about significant liquidation of domestic tuna harvesting and processing capacity, the petitioners requested an increase in the rate of duty on canned tuna imports not in oil to 35 percent for 5 years. They reasoned that such an adjustment to the tariff on tuna canned in water, together with steps taken to reduce production costs, would restore profitability to the domestic industry, and thereby enable it to implement various long-term programs designed to enhance productivity and restore its ability to compete.

The rapid and substantial increase in the volume of canned tuna imports in water began in the early 1980's when tuna canned in water started to surpass tuna canned in oil in popularity among U.S. consumers, and rising production costs within the U.S. industry brought about record high prices at the ex-vessel, wholesale, and retail levels. This combination of events, plus a disparate tariff on tuna canned in water, provided an opportunity for lower priced, low-cost imports to inundate the domestic market. As a result, imports have made significant inroads into the strongest growing segments of the U.S. tuna market, that is, tuna packed in water for sale to private label and institutional customers. Since consumers of private label and institutional packs tend to purchase on the basis of price and not brand loyalty, these market sectors are characterized by extreme price sensitivity and very narrow profit margins. To maintain a presence in these sectors, domestic processors have had to accept greatly reduced prices for their institutional and private label packs.

Even though foreign processors have concentrated on the private label and institutional sectors of the domestic canned tuna market, sales of U.S. nationally advertised brands have also been affected. As rising costs of production pushed the price of domestically canned tuna higher, the widening price spread at retail induced consumers to substitute privately labeled imported tuna at much lower prices for the more familiar advertised brands. This situation precipitated major price reductions on nationally advertised brands. Together with depressed institutional and private label revenues, price reductions on the nationally advertised brands reduced profit margins to unacceptably low levels under the industry's existing operations structure.

To offset declining revenues, domestic processors acted to lower production costs by taking advantage of latent offshore production capacity. By shifting operations from the continental United States to sites in American Samoa and Puerto Rico, processors sought to realize significant savings associated with proximity to developing fishing grounds, lower labor costs, and economies resulting from consolidating operations.

While these adjustments led to acute unemployment at continental sites, the expanded offshore production increased employment at those sites making the overall industry unemployment situation appear less severe. Also, because income generated by processing operations in American Samoa and Puerto Rico is effectively exempted from U.S. tax, and because American Samoa and Puerto Rico grant tuna processors exemptions from local tax laws, there were additional incentives to concentrate production offshore. Moreover, the move to offshore processing was accompanied by accelerated development of the western Pacific fishing grounds which contributed greatly to a rapidly growing worldwide supply of cannery grade raw tuna. This allowed further cost savings on the part of U.S. processors by enabling them to withstand any increase in the price of raw fish, and in fact, ex-vessel prices continued to decline.

In the wake of these cost reducing measures, retail prices of domestically packed canned tuna began to decline and sales started to rebound. Nonetheless, prices of imports also declined, which renewed downward pressure on domestic prices. Thus, domestic processors continued to experience substantially lower profit margins which made it extremely difficult to justify long-term investments directed toward upgrading and expanding domestic production facilities. Consequently, a strong incentive for domestic processors to become prominent importers of canned tuna has been created.

The adversities that befell domestic processors in the early 1980's filtered down to U.S. tuna fishermen in the form of significantly lower ex-vessel tuna prices and increased difficulties and delays in landing and disposing of their catches. Furthermore, processors attempted to divest themselves of interests they held in tuna vessels and to reduce financial support they had provided to independently owned vessels. This occurred during a period of soaring interest rates that left many newer vessels, financed at variable interest rates, with unmanageable debt service.

Under these conditions many vessels in the fleet were unable to participate in the fishery, and the number of inactive vessels has increased dramatically since 1982. Yet in terms of the total receipts of domestically caught tuna and the number of active vessels, cannery deliveries on a per vessel basis have improved markedly since 1982. On the other hand, gross earnings per vessel, based on the total value of domestically caught tropical tuna receipts, have not improved. These circumstances reflect the abundant supply of tuna worldwide and the influence of international market conditions on U.S. ex-vessel price negotiations.

Deterioration of vertical integration within the industry and a weakening domestic ex-vessel market have prompted owners of U.S. vessels to look further abroad for alternative tuna fishing and marketing opportunities. This is exemplified by the growing number of foreign charters, the number of flag transfers, and unparalleled exports of domestically caught tropical tuna in 1984. Exports appear to represent a particularly significant opportunity, and the potential of exports has been enhanced by development of the western Pacific fishing grounds, the proximity of these grounds to east Asian processing sites, and also by improved fishing in the eastern tropical Pacific (ETP) in 1984. The preponderance of large yellowfin tuna (>20 pounds) in ETP catches has stimulated U.S. exports to European tuna markets where such fish command a premium price. This is in contrast to the east Asian markets where, due to relatively low labor costs, there is a greater demand for smaller, lower priced yellowfin and skipjack tuna, which are relatively abundant in nearby waters.

The impact of recent events on the U.S. tuna industry has not been confined to the tropical tuna fishery. Cannery closures and relocations have threatened U.S. albacore fishermen with the virtual disappearance of their traditional market. Given this prospect, those in the albacore sector of the industry have directed a great deal of attention and effort toward developing a restaurant and retail trade for fresh or fresh frozen albacore. Successful development of a fresh/frozen market for albacore will especially benefit small-boat fishermen who, by virtue of their vessels' limited operating range, are particularly vulnerable to U.S. west coast cannery closures. On the other hand, large-boat fishermen whose operating range is more extensive, are probably in a better position to service the realigned cannery demand.

Fresh tuna products may be a viable alternative for the tropical tuna fleet as well. Bluefin, bigeye, and yellowfin tuna, are usually available within relatively close range of major population centers on the west coast where there are growing markets for these popular, high-valued, "sushi" grade tuna species. Currently, these markets are being supplied by imports and, to a large extent, by shipments from the U.S. east coast and Hawaii. These circumstances seemingly present an opportunity for market penetration by U.S. west coast tuna fishermen, particularly small-boat operators who have been especially disadvantaged by the reduction in west coast processing capacity.

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IMPACT OF CHANGING HABITATS ON LATITUDINAL VARIATIONS IN TROPHIC SYSTEMS OF TELEOSTEAN FISHES

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ABSTRACT

The trophic systems of teleostean fishes studied at Pacific-Ocean sites widely separated by latitude were more complex and involved more species towards the equator. This situation appeared linked to characteristics of the specific habitats involved rather than to more general latitudinal differences. The character of the temperate habitats was set by the dominating macroalgae and as these algae progressed through their normal life-stages the habitats experienced rapid and profound transformations. This condition favoured generalized feeders and simple trophic systems that are able to accommodate changeable and unpredictable food supplies. The character of the tropical habitats, on the other hand, was set by the dominating scleractinian corals, and, because these organisms grow and change so slowly the habitats remained relatively unchanged during the lives of most inhabitants. This condition favoured specialized feeders and complex systems that are able to develop with stable and predictable food supplies.

INTRODUCTION

It has long been recognized that plant and animal communities generally include more species at lower latitudes (e.g. Wallace 1878, Fisher 1960), which is certainly true of teleostean fishes. In this paper I link this condition to trophic relationships, which I consider are the major forces structuring fish communities (Hobson 1974). I compare trophic relationships in communities widely separated by latitude: a temperate community in Northern California (38°N), a warm-temperate community in Southern California (33°N), and a tropical community in Hawaii (19°N).

METHODS

The communities at each location have been characterized over the past 16 years by visual counts and samples from 25 x 4 m transects established in representative habitats. Prey have been identified from gut contents, and organisms potentially available as prey have been identified in samples taken with a variety of nets, corers, suction hoses, and other sampling devices (Hobson 1974, Hobson and Chess 1976).

LATITUDINAL TRENDS IN TROPHIC RELATIONSHIPS

There were more species in habitats at lower latitudes. Thus, I counted 15 species (41 transects) at the temperate site, 30 species (48 transects) at the warm temperate site, and 128 species (22 transects) at the tropical site. These differences can be linked to trophic relationships. Despite the great variety of form and habit among them, the species represented here can be grouped according to how much their feeding morphologies have diverged from that of their generalized ancestors. (Most modern reef fishes are products of a radiation from just a relatively few generalized forms early during the Cenozoic: Gosline 1959, Shaeffer and Rosen 1961, Hobson 1974).

Teleosts with trophic features relatively unchanged from the ancestral form may be highly specialized in other morphological features, but are characterized by large mouths (Fig. 1). These species are adapted to directly approach, and sieze, exposed prey that are small enough to manipulate, yet large enough to grasp, and which typically are moving when captured. Generally their prey lack heavy armour, and such components as strong spines or tough, fibrous tissues, which their unspecialized trophic systems cannot process. Among fishes in this category are most of the piscivores, as well as most species that take motile crustaceans larger than about 2% of the predator's length. Included are most members of the families Muraenidae, Synodontidae, Holocentridae, Scorpaenidae, Hexagrammidae Serranidae, Priacanthidae, Apogonidae, Carangidae, Haemulidae, Sciaenidae, Cirrhitidae, Clinidae, Gobiidae, Bothidae, and Pleuronectidae. Although species in this category were numerous in all regions studied, they constituted decreasing proportions of the fish communities toward the equator. Based on direct counts in established transects, species in this category constituted 87% of those in the temperate habitats (13 of 15; n = 41 transects), 67% of those in the warm-temperate habitats (20 of 30; n = 48 transects), and 21% of those in the tropical habitats (27 of 128; n = 22 transects).

Most species that belong to groups which have diverged from the main teleostean line on the basis of specialized trophic characteristics are distinguished by adaptations that cope with specific types of defences in prey. Three major subcategories are evident: predators on sedentary prey, herbivores, and diurnal planktivores. They are distinguished by such characteristics as strong jaw and pharyngeal teeth adapted to crush heavy armour (Fig. 2), protruding snouts adapted to reach prey hiding in narrow crevices (Fig. 3), small mouths with dentition adapted to pluck prey too small to be taken by the generalized predator's large mouth (Fig. 4), and digestive systems capable of processing noxious tissues (Fig. 5). Species with such characteristics include members of the Chaetodontidae, Pomacanthidae, Kyphosidae, Pomacentridae, Embiotocidae, Labridae, Scaridae, Acanthuridae, Blenniidae, Monacanthidae, Tetraodontidae, and Canthigasteridae. Of these families, all but the Embiotocidae are primarily tropical or subtropical. They include 20% of the species counted in the temperate habitats (3 of 15), 33% of the species counted in the warm temperate habitats (10 of 30), and 79% of the species counted in the tropical habitats (101 of 128). Species in this category account for most of the increased number of species toward the equator, and for most of the greater complexity of trophic interactions at lower latitudes.

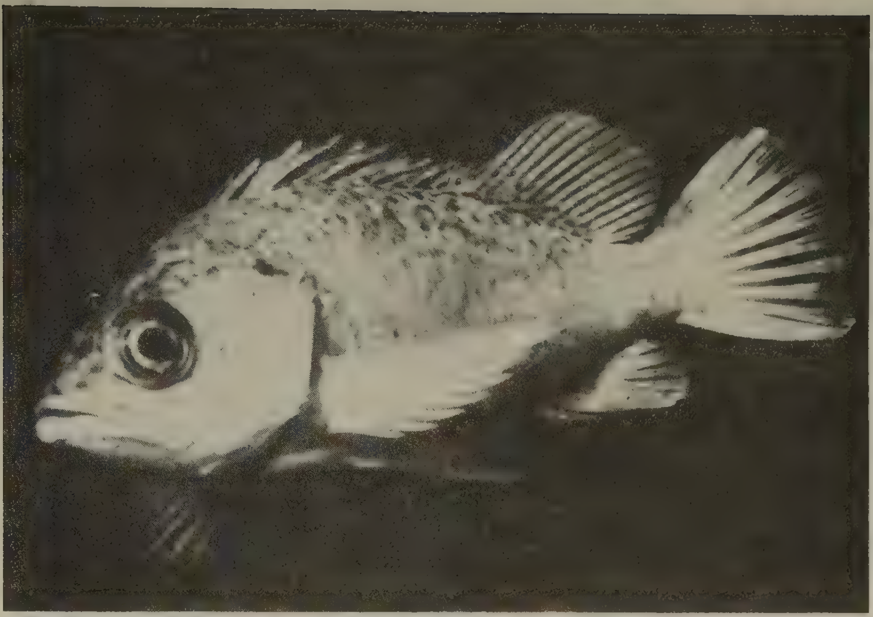

Figure 1. The Kelp rockfish, Sebastes atrovirens, of the family Scorpaenidae in Southern California, has the large mouth of a generalized predator.

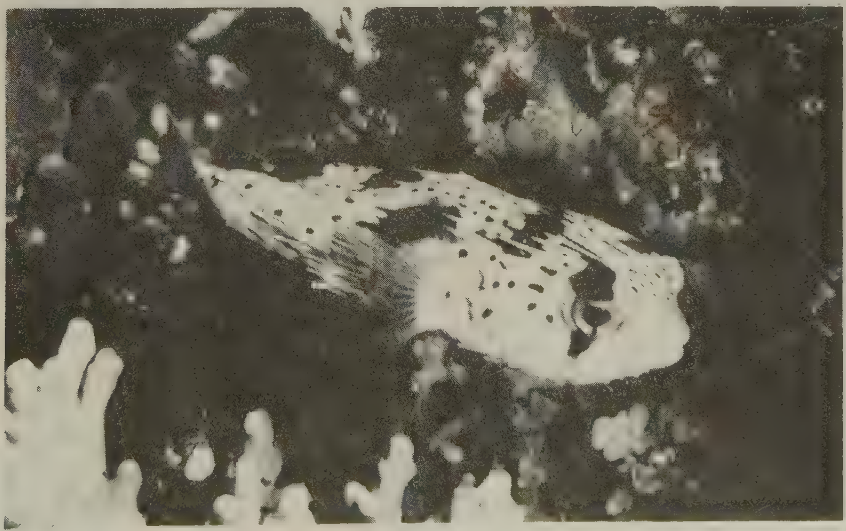

Figure 2. The porcupine fish, Diodon holacanthus, of the family Diodontidae in Hawaii, has heavy beak-like jaws suited to crush shelled organisms.

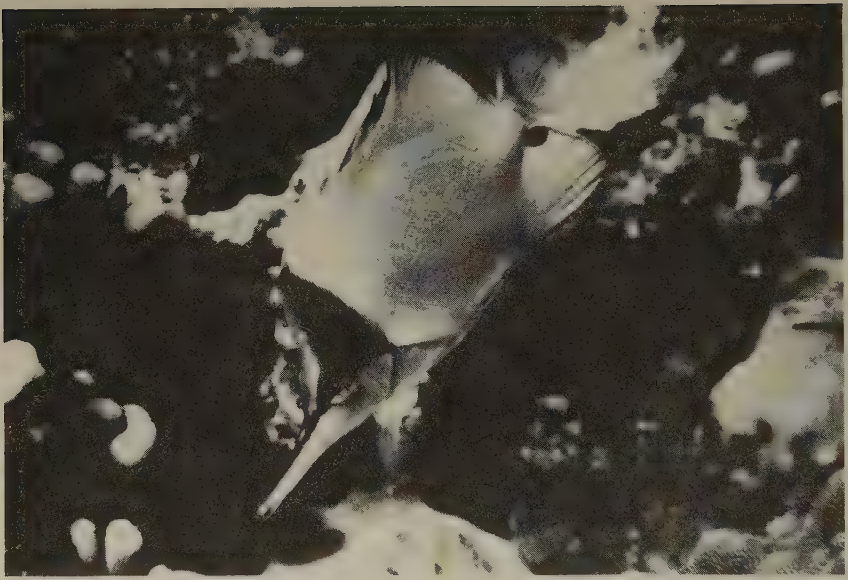

Figure 3. The long-nosed butterflyfish Forcipiger flavissimus, of the family Chaetodontidae in Hawaii, has an elongated snout suited to probe reef crevices for sheltered prey.

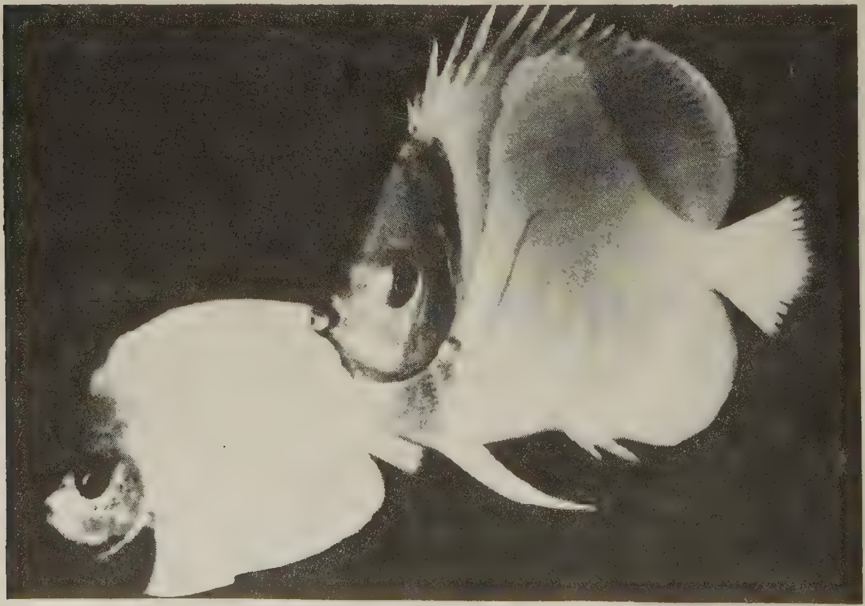

Figure 4. The pyramid butterflyfish Hemitaurichthys polylepis, of the family Chaetodontidae, has a small mouth and dentition suited to take the tiny zooplankters that are its major prey.

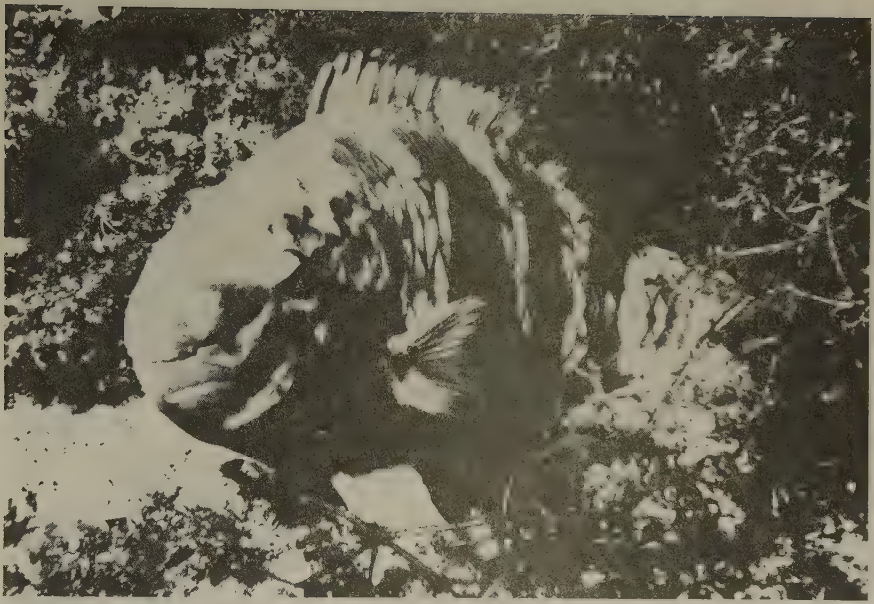

Figure 5. The bluechin parrotfish Scarus ghobban, of the family Scaridae in the Gulf of California. The beak-like dentition of this fish is suited to scrape algae from rock surfaces, and its digestive system is specialized to digest this material.

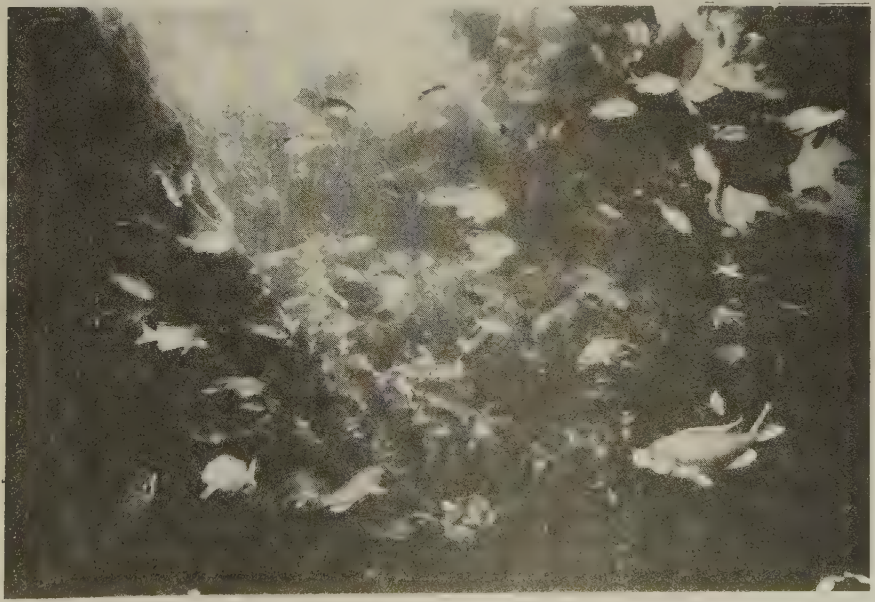

Figure 6. This and other habitats dominated by macroalgae in Southern California (33°N) experienced frequent and profound transformations during 13 years of study (1972-1985). The fish are Chromis punctipinnis, a diurnal planktivore.

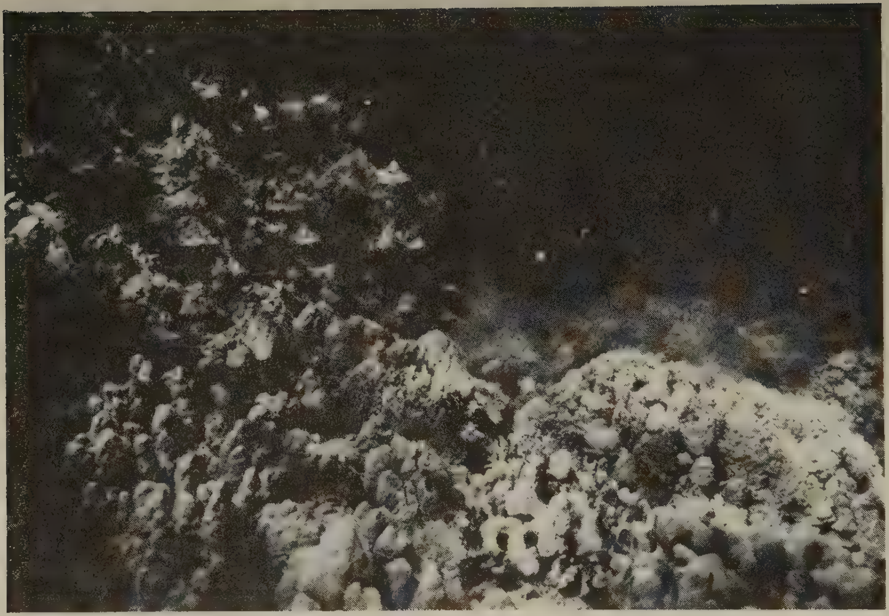

Figure 7. This and other habitats dominated by scleractinian corals in Hawaii (19°N) remained virtually unchanged during 15 years of study (1969-1984).

DISCUSSION

There are probably multiple and complex reasons why communities tend to be more diverse at lower latitudes (see Pianka 1966, and MacArthur 1969, for reviews of hypotheses). It is widely recognized that tropical communities include more specialized species (e.g. Cowell 1973), but some investigators (e.g. Sale 1976) doubt that increased specialization is the basis for tropical diversity. In the communities examined here, however, it was clear that the increased number of species at lower latitudes involved mostly specialized feeders. But in these cases the condition seemed to relate to characteristics of the specific habitats involved, rather than to more general latitudinal characteristics.

The pattern of trophic relationships defined in this paper appeared strongly influenced by the normal life-history stages of the predominating biological features of the respective habitats. The temperate and warm-temperate sites are dominated by benthic macroalgae (Fig. 6), and experience profound transformations associated with the rapidly progressing life-stages of these plants. The effect is more pronounced in the temperate habitats because the major alga there, Nereocystis leutkeana, is an annual, whereas the major alga in the warm temperate habitats, Macrocystis pyrifera, is a perennial. On the other hand, the tropical sites are dominated by scleractinian corals (Fig. 7), and experience comparatively little change because these organisms grow so slowly. It may be because conditions in the coral-dominated habitats at lower latitudes remain comparatively unchanged during the lives of so many inhabitants that the fish communities there include more species with specialized trophic features, and more complex trophic systems. Probably such community characteristics are limited in the algae-dominated habitats at higher latitudes by the frequent and profound changes that prevail there. Favoured instead should be more generalized trophic features, and simpler trophic systems, that can accommodate changeable and unpredictable food supplies.

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PREDATION ON THE PACIFIC SAND LANCE, *AMMODYTES HEXAPTERUS* (PISCES: AMMODYTIDAE), DURING THE TRANSITION BETWEEN DAY AND NIGHT IN SOUTHEASTERN ALASKA.—

The Pacific sand lance, *Ammodytes hexapterus,* is particularly vulnerable to predators during a changeover between distinctive diurnal and nocturnal modes of behavior. This conclusion developed from observations in southeastern Alaska during 10 days of May 1978. At that time, sand lance (110–150 mm SL) were attacked by a variety of predators in a small cove (area about 2 ha, maximum depth about 25 m) at the head of Steamer Bay, Etolin Island (56°N, 133°W). Twelve hours of general observations spread over the diel cycle showed predation on sand lance concentrated during the transition between day and night. Between 1800, when diurnal conditions still prevailed and 0030, when nocturnal conditions had been in force for some time, I spent 5 hr over five evenings observing interactions between sand lance and specific predators. (No observations were made during the morning changeover between night and day.)

Intensified evening predation occurred while most of the sand lance were moving from an active mode in the water column to a resting mode in the sediments. This changeover was part of a diel pattern of movements between a feeding ground, nearby schooling sites and a refuge in the sand. The feeding ground was at the cove's entrance, where the sand lance foraged when tidal currents flowed into the cove during the day. At these times the sand lance joined Pacific herring, *Clupea harengus pallasi,* in mixed aggregations and fed vigorously on zooplankton throughout the upper levels of a 10 m water column. (A planktivorous diet appears to be characteristic of *Ammodytes* spp., Macer, 1966; Reay, 1970; Scott, 1973.) At other times of the day most of the sand lance were in dense, monospecific schools that moved slowly several meters above the bottom, within about 100 m of the cove's entrance. Feeding by members of these schools was much reduced and limited to individuals at the schools' edges. Often the schools were near one particular patch of coarse sand, about 0.1 ha in area, that sloped sharply between depths of about 5 and 10 m near shore, approximately 75 m from the cove's entrance. Except at this one spot the cove was floored by silt, fine sand, gravel, cobble and larger rocks. The patch of coarse sand was the sand lance's refuge, probably because it was a relatively loose, porous substrate conducive to burrowing. Reportedly similar sediments are refuges for *A. americanus,* an Atlantic Ocean species (Meyer et al., 1979).

Using the numbers of sand lance flushed when the substrate was disturbed as an index to the numbers buried, it was determined there were at least some in the sediments of the refuge at all times during the diel cycle. (Often sand lance were flushed when I simply swam close to the bottom.) Relatively few were there by day, however, while at night these sediments seemed to contain virtually all the sand lance in the cove. Widespread inspection of sediments elsewhere in the cove after dark flushed only an occasional individual and extensive search of the nocturnal water column found none. Describing a similar situation in the Baltic Sea, Kühlmann and Karst (1967) reported that almost all the sand lance in their study area foraged offshore during the day and burrowed in one particular nearshore sand bank at night.

It was difficult to determine when the evening changeover began. Sunset was at about 2200 (Pacific Daylight Savings Time; Nautical Almanac, US Naval Observatory), but could not be observed on the evenings involved here owing to either clouds at the study site or my being underwater at the time. Nevertheless, daylight was greatly diminished underwater by 2030, when the sand lance moved in several small schools over central parts of the refuge where I had not seen them earlier in the day. Periodically, these schools descended to within a meter of the substrate, at which point individuals and small groups dove from the schools into the sand.

At about the same time, predators began to concentrate in the refuge and to station themselves under the slowly moving schools. Four species of predators were consistently present: rock sole (*Lepidopsetta bilineata*), starry flounder (*Platichthys stellatus*), great sculpin (*Myoxocephalus polyacanthocephalus*) and whitespotted greenling (*Hexagrammos stelleri*). All four are sedentary forms that attack from positions at rest on the substrate. Although numerous in the refuge when sand lance were entering the sediment in large numbers, the predators were not concentrated there during observations made at other times.

As the sand lance schools moved slowly over the refuge, the predators followed along beneath them and intensified their attacks. The predators, however, did not strike at individuals that were in the schools or in the act of diving into the sand. Rather, they struck at individuals that had entered the sand, but which appeared to be having difficulty settling into a resting spot. The sole and flounder seemed responsive to movements of the sand above restless sand lance and attacked by driving their jaws into the sand, whereas the sculpin and greenling went after sand lance that reappeared after having been buried. These prey of sculpin and greenling may have found their initial resting spots unsatisfactory, because they soon emerged and swam off to settle again elsewhere, or to rejoin the schools. Often these emerging sand lance paused with head protruding from the sediment—perhaps to look for threatening predators. Then, with a vigorous move, they cleared the bottom and darted away. The sculpin and greenling struck the moment the sand lance emerged from the sand, suggesting their attacks may be even more intensive during the morning changeover, when presumably most of the sand lance emerge from the sand.

One sole (328 mm SL) was speared after it had been seen striking four times at buried prey in the refuge. Its gut contents included four sand lance (about 110 mm SL), but only two of these were fresh enough to have been recently captured. The other two were extensively but similarly digested, indicating they had been captured during some earlier feeding period (perhaps early that morning). The rest of the gut contents, which were in varying stages of digestion and so probably represented feeding throughout the day, consisted of six polychaetes (30–110 mm long) and four limpets (5–10 mm). One sculpin (150 mm SL), speared after attacking an emerging sand lance, contained two of them—one (115 mm) apparently recently captured and the other (about 100 mm SL) extensively digested.

Although certain sand lance seemed vulnerable during initial adjustments to the resting mode, once settled in they appeared secure. This became evident when the predators continued to limit their attacks to sand lance that had just entered the sand, even after buried sand lance became numerous throughout the area. Buried sand lance in the Baltic Sea were similarly judged by Kühlmann and Karst (1967) to be secure from predators throughout the night.

Predation continued unchanged through the developing twilight, except that the sand lance schools became progressively smaller. Although individuals at the edges of the schools sporadically snapped at zooplankton, feeding seemed relatively insignificant during the changeover. I observed small schools of sand lance above the refuge as late as 2230, but on that occasion an exhausted air supply forced me to leave the site. When I returned 30 min later, sand lance no longer occupied the water column and most of the predators were gone. This situation was still in effect when I left the site at 0030.

Despite the limited scope and duration of these observations, probably they have widespread relevance. For example, the diel activity pattern in *A. hexapterus* had many elements in common with the diel pattern of sand lance in the Baltic Sea (as described by Kühlmann and Karst, 1967). Probably at least most species of sand lance change from an active to an inactive mode during the transition between day and night. Although nocturnally active sand lance have been reported (Senta, 1965), Winslade (1974:574) suggested these may have been individuals drawn from the sea floor by "bright lights of the observing ship." Sand lance are known to be attracted to light at night (Borisov, 1955, cited in Winslade, 1974), but presumably sand lance drawn to lights at the water's surface from resting places on the bottom were not completely buried in the sediment. Probably some keep at least one eye uncovered, which would account for the numbers flushed from the sand when I swam close to, but did not come in contact with, the bottom. Describing the nocturnal behavior of *A. marinus* (an Atlantic Ocean species) in aquaria, Winslade (1974) noted that although most individuals were completely buried in the sand, a few were partially uncovered.

Vulnerability to predators during a changeover between distinctive diurnal and nocturnal modes of behavior is widespread among fishes, but most evidence comes from the tropics (Hobson, 1968; Munz and McFarland, 1973; Major, 1977). If there is a comparable period of crepuscular vulnerability at higher latitudes one would expect it to be extended by the longer twilight there. According to Helfman (1981), the poleward increase in length of twilight explains why temperate lake fishes spend more time than do tropical reef fishes shifting between their diurnal and nocturnal modes. That changeover times increase with latitude was evident in Steamer Bay, where the 2 hr *A. hexapterus* spent in transition more than doubled the changeover period involving all the fishes—both diurnal and nocturnal—on coral reefs in tropical Hawaii (as described by Hobson, 1972). This difference can be related to the lengths of twilight at the two locations. On the dates of the observations involved, Civil Twilight lasted 57 min in Steamer Bay, compared to a mean of about 23 min in Hawaii (Nautical Almanac, US Naval Observatory). And as might have been predicted from this difference, *A. hexapterus* in Steamer Bay experienced intense crepuscular predation over a period that more than doubled the reported duration of intense crepuscular predation on fishes in tropical seas (Hobson, 1968; Major, 1977).

Probably it is at least partly a latitudinal difference that more than ⅔ of the changeover and related predation experienced by *A. hexapterus* occurred before sunset, whereas most of the changeover events among fishes on tropical coral reefs occur after sunset (Hobson, 1972; McFarland et al., 1979). This difference should have been expected if, as most reports have suggested (Collette and Talbot, 1973; Domm and Domm, 1973), the changeover events are a response to specific levels of decreasing daylight, rather than to time of sunset. Daylight faded much earlier relative to sunset in Steamer Bay than it does on tropical coral reefs, not only because the water was less transparent, but also because the sun was low in the sky—virtually on the horizon—for a much longer period immediately before sunset.

The surge in predation among fishes during the transition between day and night is to some extent a consequence of successful adaptations to the two major segments of the diel cycle. Because day and night are so different, appropriate adaptations to each have resulted in widely divergent modes that must be bridged during twilight. Thus, over the diel cycle, *Ammodytes* spp. effectively reduce predation two very different ways—by day they school (Pitcher and Wyche, 1983) and by night they burrow (Kühlmann and Karst, 1967). And as the crepuscular attacks on *A. hexapterus* in Steamer Bay have demonstrated, the transition between these two modes can be perilous.

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Diel Movements of Resident and Transient Zooplankters Above Lagoon Reefs at Enewetak Atoll, Marshall Islands[1]

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ABSTRACT: Of those zooplankters above reefs on the lagoon shelf at Enewetak Atoll at some time during the diel cycle, the vast majority of those larger than about 1.5 mm were there only at night. Many of these larger forms were local residents that by day sheltered in or near shelf substrata, or in swarms close to these substrata, and at night made purposeful forays above the shelf. Many others, however, were transients from the deeper regions of the lagoon, or from the open sea outside the atoll, and these were above the shelf at night by chance. The residents included various polychaetes, cypridinacean ostracods, copepods, mysids, tanaids, isopods, amphipods, and carideans. The transients were mostly holoplankters that included halocyprid ostracods, calanoid copepods, euphausids, and chaetognaths. Both residents and transients were above the shelf at night as a result of diel vertical migrations. The residents were adapted to stay within reach of their diurnal habitats while in the nocturnal water column, often by avoiding currents, and so were readily able to return to those habitats at dawn. The open-water transients, however, lacked such adaptations, and, as a result, probably many were stranded in the shallows above the shelf at dawn, unable to return to their daytime depths and probably vulnerable to planktivorous fishes.

ASSEMBLAGES OF ZOOPLANKTERS above tropical reefs differ from day to night. Most of these differences stem from diel movements of organisms that rise or disperse in the water column only after dark (see Emery 1968; Hobson and Chess 1978). Some of these nocturnal forms are residents of the reef area, whereas others are transients from other habitats. Diel patterns in each of the two groups are distinctive. By day most of the residents are either benthonic (Alldredge and King 1977; Hobson and Chess 1979) or aggregate in dense swarms close to benthic substrata (Hamner and Carleton 1979). The transients, in contrast, are mostly offshore holoplankters that are carried or disperse shoreward after rising toward the surface at night from deeper water (Hobson and Chess 1978).

Although these diel patterns are apparent from existing literature, there remains need for study at the species level in specific environments. Here we consider the patterns as they occur among zooplankters in the lagoon at Enewetak Atoll (11°26′N, 162°22′E). The study concerns those organisms that at some time during the diel cycle occurred above the shelf of sand and isolated patch reefs on the windward side of the lagoon. We consider all the varied forms which were collected in our plankton nets or traps and which belong to groups included in most general accounts of the zooplankton (such as Newell and Newell 1963; Wickstead 1965).

The goals of the study were twofold: to define the diel patterns of occurrence of zooplankters above patch reefs on the lagoon shelf and to determine which of them were residents of the shelf habitat and which were transients from the open sea or the deeper waters of the lagoon.

COLLECTING SITES

We sampled the zooplankton on the windward side of the lagoon where the shelf is one

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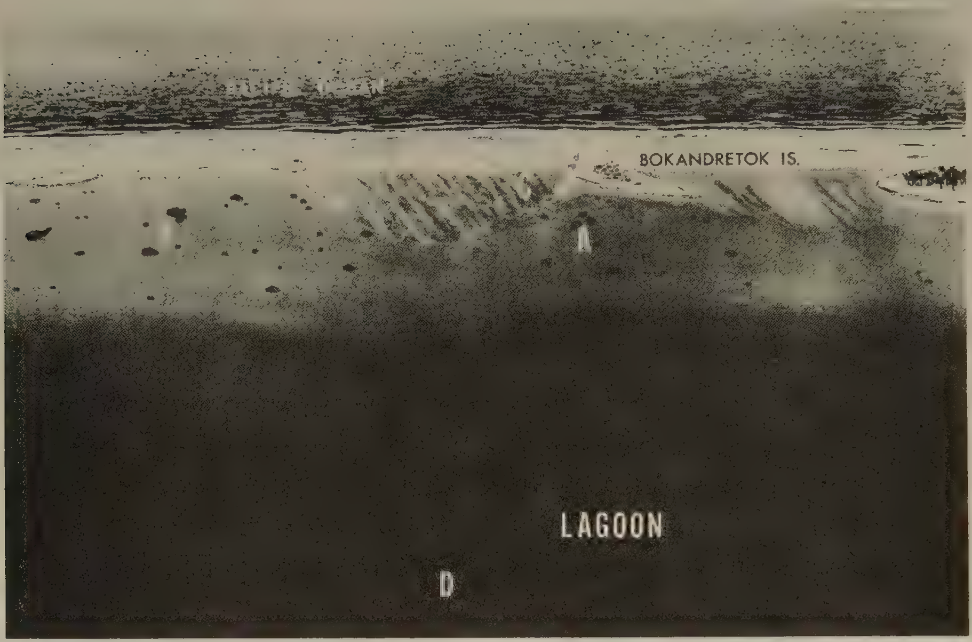

FIGURE 1. The study area on the windward lagoon shelf at Enewetak Atoll, with collecting stations designated. Station A is in the path of intermittent currents that bring water from the open sea across a low point in the interisland reef. Station B is protected from such currents by a high point on the interisland reef that remains exposed even at high tide. Station C is on the interisland reeftop, upcurrent from Station A. Station D is offshore in the lagoon, beyond the shelf.

to several hundred meters wide and under 5 to 15 m of water (Figure 1). At the outer edge of the shelf the bottom falls away sharply to depths of 30 to 50 m, which is the approximate water depth over much of the lagoon. Currents over the shelf consist of water that has flowed across the interisland reef from the open sea. This cross-reef flow is variable, depending on the height of the tide and the surf breaking on the ocean side, but it moves in just one direction—into the lagoon (Atkinson et al. 1981).

Zooplankton were sampled at or near four stations (Figure 1): Stations A and B were above the shelf, Station C was above the interisland reef, and Station D was in the deeper water of the lagoon, beyond the shelf. The collections at and near Stations A and B determined the composition of zooplankton assemblages above the lagoon shelf at different periods of the diel cycle. Because the distribution of these zooplankters was certain to be influenced by water currents, the two stations were positioned to sample contrasting examples of the highly variable current conditions that prevailed above the shelf.

Station A, which faced a low section of the interisland reef across which water flowed from the open sea during higher tides, was intermittently swept by currents of up to 25 cm/sec^{-1}. Although usually this flow was blocked by the exposed reef at low tide, even on the lowest tides the trade winds, or high seas breaking outside the atoll, sometimes drove enough water across the reef to generate currents on the shelf. When the wind shifted just a few degrees to the south, however, the current was deflected northward by Bokandretak Island, and Station A was in an extensive area of quiet water that persisted in the lee of that island (Figure 1). Station A encompassed a pair of patch reefs (both approximately 5 × 10 m), a few meters apart, in about 5 m of water.

Station B was sheltered from tidal currents by a high section of the interisland reef that was above water at all stages of the tide (Figure 1). Generally we were unable to detect a current at this station, although a lagoonward drift of a few cm/sec^{-1} sometimes was evident above the shelf a short distance offshore when high tides were backed by the usual strong trade winds. The station encompassed a pair of patch reefs (approximately 3 × 5 × 5 and 3 × 5 × 15 m), just a few meters apart, in about 5 m of water.

Station C was in water flowing across the interisland reef from outside the atoll on the higher tides and thus sampled the zooplankters that were entering the lagoon from the open sea.

Station D was in the deeper waters of the lagoon, and here we sampled zooplankters during the day to identify species likely to be among those from that habitat which joined the zooplankton above the shelf after dark.

COLLECTING METHODS

Most of the collections were made using SCUBA, so that we directly observed the conditions under study. And because the work was concentrated during 3 weeks of May and June 1979, we avoided many of the variables associated with changing seasons, such as seasonal differences in species composition (as reported from Enewetak by Gerber 1981).

To sample organisms in the water column (except at Station C), we pushed a net mounted in a square frame (78 × 78 cm) over an established course, each time for 10 min at a speed of about 30 cm/sec^{-1} (Hobson and Chess 1976, 1978), so that each of the collections filtered about 110 m^3 of water. The 0.333-mm mesh of this net, however, did not effectively sample zooplankters smaller than about 1 mm. Hence to gain some measure of organisms lost through the mesh of our standard net, we paired it in a limited number of collections with a net of 0.165-mm mesh set in a 0.5-m ring. Our standard net had the square frame rather than the usual circular frame because the square configuration was more effective close to the sea floor and the water's surface—two important concerns when sampling shallow-water zooplankton (Hobson and Chess 1978: fig. 2).

Because we swam with the nets during most of the collections, guiding them throughout, we sampled precisely defined locations and were able to observe many of the organisms in the path and immediate vicinity of the net. Thus we knew whether or not certain of the larger, more mobile organisms evaded our net. Mysids, for example, were among the more elusive forms, but even these escaped less often than might be expected owing to their mobility. Much of the time our net enveloped mysids without eliciting an evasive response, probably because the net's approach was relatively slow and quiet and its opening was unobstructed by the tethering gear that usually precedes a plankton net. We considered the unobstructed opening more important than an absolute measure of the volume of water filtered and thus did not use a flowmeter. The questions asked demanded only that the collections be comparable with each other, and this demand was met.

To identify those primarily benthic organisms that periodically left the shelf floor and joined the zooplankton, we placed traps on the three major shelf substrata—sand, rubble, and patch reef—in the vicinity of Stations A and B (Figure 2).

The traps used in sand and rubble were identical to the trap illustrated earlier (Hobson and Chess 1979: figs. 1 and 2; see that paper for details on how the traps worked), but these devices were unsuitable for use on the hard, irregular surfaces of the reef because their rigid metal bases required a bed of sediment. To sample the patch reefs, we used a trap that had as a base a pliable canvas skirt that could be folded over to form a continuous pocket. Once the base was in position on the reef, we loaded the pocket with bags of lead shot (approximately 18 kg) and then sealed it by adjoining a series of Velcro strips sewed to its edges. The base, which now matched the contours of the reef (and thus made a good seal with the reef), also provided an effective anchor (Figure 2: trap on the right).

Additional information on the sampling stations and the collection procedures is given below, where each element of the study is recounted in detail.

DIEL OCCURRENCES OF THE ZOOPLANKTERS ABOVE THE LAGOON SHELF

To characterize the diel occurrences of zooplankters above the lagoon shelf, we made ten pairs of collections with the standard plankton net at Stations A and B: four pairs by day and six pairs at night—a total of 20 collections. Each pair consisted of a collection at one station followed within 30 min by a collection at the other. At each station we always followed the same course, continously moving up and down between surface and bottom. The nocturnal collections were made without diving lights, because these are known to attract certain zooplankters and because natural light in these clear waters over white sand was sufficient to navigate even on moonless nights. The collections sampled day and night during high and low spring tides and also high and low neap tides. They also spanned all periods of the night, from 1 hr after sunset to 1 hr before sunrise, and through that part of the lunar cycle from new moon to three-quarter moon. The daytime collections were made between 1030 and 1600 hr.

These collections (Table 1) were judged to document the diel occurrences of zooplankters of about 1 mm in size and larger. Zooplankters smaller than this were poorly sampled by our standard net, however, a fact made clear by collections that paired this net with one of finer mesh (Table 2). So the material that follows, except where specified, refers to zooplankters 1 mm in size and larger.

At both stations, many more zooplankters were taken at night than during the day (Wilcoxon two-sample test: $Z = -3.67$, $p = 0.0001$). Furthermore, virtually all of the zooplankters larger than 2 mm in their greatest dimension were in the nocturnal collections. Included were species that belong to groups widely recognized as benthonic during much of the diel cycle, such as polychaetes, mysids, cumaceans, tanaids, isopods, amphipods, and natantians. Also included were species of groups widely considered to be in the water column throughout the diel cycle, such as calanoid copepods and chaetognaths. It was clear that during the day most of the larger zooplankters were somewhere other than in the water column above the lagoon shelf. It was equally clear that many smaller zooplankters (<1 mm) did not follow this pattern, as they were abundant in these waters day and night (Table 2).

Had these collections been made with nets deployed from a vessel there would have been uncertainty whether the absence of larger (and therefore more mobile) forms meant they were in fact absent from the water column or whether daylight had simply allowed them to evade the net. But our direct observations in the environment throughout the diel cycle confirmed the collection results: the larger zooplankters generally were present in the water column above the shelf only at night.

Thus a major question was: where were the larger zooplankters during the day? Having identified the three obvious possibilities earlier (Hobson and Chess 1978), we set out to determine which of them had arrived above the patch reefs at night from daytime positions in, on, or close above the shelf, which of them had come over the interisland reef from the open sea, and which had come from the deeper waters of the lagoon.

ZOOPLANKTERS THAT SHELTERED ON THE SHELF

Our traps set on shelf substrata within 50 m of Stations A and B sampled organisms that entered the water column at some time during the diel cycle from benthic habitats on the shelf. The collections involved sets of three traps placed close together, each trap sampling one of the three major substrata: sand, rubble, and reef (Figure 2). Although the trap collections were designed to sample the major benthic habitats on the shelf, they did not effectively distinguish organisms associated with specific substrata. Only the sand collections represented what approximated a single substrate type. The rubble collections actually sampled a combination of rubble and sand, whereas the reef collections sampled combinations of all three substrata.

TABLE 1

ZOOPLANKTERS COLLECTED ABOVE THE LAGOON SHELF AT ENEWETAK ATOLL, DAY AND NIGHT[*]

	DAY					NIGHT				
		STATION A (INTERMITTENT CURRENT) $N = 4$		STATION B (NO CURRENT) $N = 4$			STATION A (INTERMITTENT CURRENT) $N = 6$		STATION B (NO CURRENT) $N = 6$	
ORGANISM	SIZE (mm)	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	SIZE (mm)	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.
Foraminiferans	0.3–1.5	100	61.1	100	17.3	0.3–1.5	100	232.4	100	100.9
Tretomphalus sp.	0.4–0.8	100	22.5	25	1.2	0.4–0.8	100	191.3	100	77.0
Discorbis sp.[†]	0.3–0.5	100	33.5	100	15.0	0.3–0.5	100	29.7	100	13.7
Cymbaloporella sp.	1.0–1.5	—	—	—	—	1.0–1.5	17	0.3	50	1.6
Globigerina sp.	0.3–0.4	75	4.5	50	0.8	0.3–0.4	33	0.3	50	2.3
Others	0.3–1.0	25	0.6	25	0.3	0.3–1.0	100	10.8	100	6.3
Polychaetes	—	—	—	—	—	0.5–12.0	100	27.0	100	22.4
Opheliids	—	—	—	—	—	3.0–12.0	50	23.0	33	11.5
Nereid epitokes	—	—	—	—	—	4.0–6.0	—	—	17	1.3
Undetermined	—	—	—	—	—	0.5–8.0	50	4.0	67	9.6
Veligers	0.4–1.2	100	57.3	75	4.0	0.4–1.3	100	37.0	100	32.3
Ostracods	0.8–1.5	25	0.5	25	0.5	0.5–3.0	100	80.5	100	95.6
Cypridinaceans	0.8–1.5	25	0.5	—	—	0.5–3.0	100	78.8	100	95.6
Halocyprids	—	—	—	25	0.5	1.0	33	1.7	—	—
Calanoids	0.8–2.0	100	44.8	100	17.8	0.7–4.0	100	422.8	100	1249.0
Acartia negligens	1.0	100	22.3	100	11.8	1.0	83	22.0	83	17.8
Undinula vulgaris	2.0	—	—	17	0.5	2.5–3.5	83	259.7	83	147.0
Calanopia minor	1.5	—	—	17	0.3	1.1–1.3	100	28.3	100	1013.0
Eleven others[‡]	0.8–1.5	50	1.3	50	1.3	1.5–4.0	83	69.5	100	46.5
Undetermined	1.0–2.0	100	21.2	50	4.9	0.7–3.0	67	43.3	100	24.7
Cyclopoids	0.7–2.0	100	19.8	100	6.4	0.8–1.5	83	16.4	83	17.3
Corycaeus sp.	0.7–1.0	100	16.3	50	1.3	0.8–1.0	50	13.3	17	14.0
Oncaea sp.	1.0	—	3.0	—	—	1.0	17	0.7	17	1.0
Oithona sp.	1.0	—	—	50	4.8	1.0	33	1.7	17	1.0
Sapphirina sp.	1.2–2.0	50	0.5	25	0.3	1.0–1.5	17	0.7	33	1.3
Harpacticoids	0.5–1.0	75	3.0	25	4.9	0.5–1.5	100	73.1	100	52.5
Peltidiids	0.8–1.0	25	0.2	25	0.3	0.8–1.0	67	5.6	50	8.0
Metis holothuriae	0.5	75	1.5	—	—	—	—	—	—	—
Tegastids	0.5	25	0.8	25	0.3	0.5	50	2.7	17	0.5
Undetermined	0.6–1.0	25	0.5	25	4.3	0.6–1.5	83	64.8	100	44.0
Mysidaceans	2.0–4.0	100	109.8	100	12.8	1.5–7.0	100	6679.9	100	5810.2
Anisomysis spp.[§]	4.0	25	5.0	—	—	4.0–7.0	100	235.3	100	206.5
Pseudanchialina inermis	—	—	—	—	—	3.0–4.0	67	848.3	83	1346.7
Siriella spp.[¶]	—	—	—	—	—	5.0–7.0	33	1.7	50	3.0
Gastrosaccus bengalensis	—	—	—	—	—	4.0	17	1.3	17	4.0
Undetermined juveniles	0–4.0	100	104.8	100	12.8	1.5–3.0	100	5593.3	100	4250.0
Cumaceans	—	—	—	—	—	1.0–2.0	100	135.3	83	18.2
Tanaidaceans	0.5–2.5	50	2.0	—	—	1.5–4.0	100	19.4	50	6.9
Leptochelia sp.	0.5–2.5	25	1.0	—	—	2.0–4.0	100	17.7	50	4.4
Tanais sp.	1.0	25	0.7	—	—	1.5	17	—	50	0.5
Undetermined	1.0	25	0.3	—	—	1.5	33	1.7	17	2.0
Isopods	—	—	—	—	—	1.0–10.0	100	21.3	100	17.3
Epicaridean larvae	—	—	—	—	—	1.0–2.0	33	3.0	83	9.3
Gnathiid females and juveniles	—	—	—	—	—	2.0–3.0	100	17.0	50	8.0

TABLE 1 (*Continued*)

	DAY					NIGHT				
		STATION A (INTERMITTENT CURRENT) $N = 4$		STATION B (NO CURRENT) $N = 4$			STATION A (INTERMITTENT CURRENT) $N = 6$		STATION B (NO CURRENT) $N = 6$	
ORGANISM	SIZE (mm)	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	SIZE (mm)	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.
Anthurids	—	—	—	—	—	4.0–10.0	33	0.3	—	—
Sphaeromatids	—	—	—	—	—	2.0	17	0.7	—	—
Cirolanids	—	—	—	—	—	1.5	17	0.3	—	—
Gammarideans	1.0–1.5	50	1.0	—	—	0.7–6.0	100	82.4	100	9.6
Synopia variabilis	—	—	—	—	—	2.0–4.0	17	—	50	3.2
Maera sp.	—	—	—	—	—	3.0–4.0	67	4.0	17	0.2
Aorids	—	—	—	—	—	1.5–2.5	50	57.0	—	—
Seven others#	1.5	25	0.5	—	—	2.0–6.0	67	3.4	33	0.4
Undetermined	1.0	25	0.5	—	—	0.7–5.0	100	18.0	50	5.8
Euphausiids	0.8	—	—	25	0.5	0.6–9.0	33	5.2	50	2.7
Calyptopis larvae	0.8	—	—	25	0.5	0.6–0.7	33	3.5	17	2.0
Pseudeuphausia latifrons	—	—	—	—	—	4.0–9.0	33	1.7	50	0.7
Natantian larvae	1.0–4.0	100	19.5	100	13.5	1.0–7.0	100	467.6	100	770.0
Natantian postlarvae	—	—	—	—	—	3.0–15.0	100	53.2	100	34.0
Ogyrides sp.	—	—	—	—	—	4.0	50	6.7	100	13.8
Alpheids	—	—	—	—	—	4.0–6.0	16	0.3	—	—
Other carideans	—	—	—	—	—	3.0–7.0	100	39.7	100	15.5
Lucifer sp.	—	—	—	—	—	8.0–13.0	67	6.2	33	4.7
Other penaeids	—	—	—	—	—	15.0	16	0.3	—	—
Zoeae	0.5–2.0	100	22.5	75	5.3	0.4 2.0	100	860.0	100	931.7
Megalopae	—	—	—	—	—	1.0 4.0	100	37.0	100	21.7
Chaetognaths**	3.0–8.0	75	13.5	25	0.5	4.0–31.0	83	124.7	100	103.0
Larvaceans	2.0–3.0	25	0.8	25	0.5	3.0–4.0	33	22.7	33	47.3
Fish eggs	0.5–3.0	100	131.0	100	136.3	0.5–3.0	100	197.3	100	288.3
Fish larvae	2.0–6.0	50	0.5	75	1.0	0.5–15.0	100	45.7	100	48.3
Miscellaneous††	—	—	6.5	—	3.8	—	—	30.9	—	14.4
$\bar{x}$ Zooplankton volume		0.5 ml		0.3 ml			10.6 ml		9.4 ml	
$\bar{x}$ Algae volume		10.7 ml		2.7 ml			1.6 ml		0.4 ml	
$\bar{x}$ Total		11.2 ml		3.0 ml			12.2 ml		9.8 ml	

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* Includes taxa where mean number of individuals taken at any station day or night was greater than 0.5.

† We base our identification of *Discorbis* sp. on Cushman et al. (1954). Apparently this is a benthic form, as many individuals (not counted) were attached to the fragments of benthic algae in our collections. According to Myers (1943), *Discorbis* (and other genera) are the benthic stages of the planktonic *Tretomphalus* spp., but the nominal designation is retained here to emphasize the ecological distinction, which is more important to this study.

‡ Other calanoids included *Acrocalanus monachus*, *Candacia* sp., *Centropages* sp., *Euchaeta rimana*, *Labidocera laevidentata*, *Pleuromamma abdominalis*, *P. xiphias*, *Pontellina plumata*, *Scolecithricella* sp., *Tortanus* sp., and *Undinula darwini*.

§ Including *Anisomysis constricta*, *A. enewetakensis*, and *A. chessi* (Murano 1983).

¶ Including *Siriella affinis* and *S. aequiremis*.

Other gammarideans included *Cerodocus* sp., *Elasmopus* sp., *Ronco sosa*, amphilochids, amphithoids, leucothoids, and stenothoids.

** Chaetognaths included *Sagitta bedfordii*, *S. enflata*, *S. ferox*, *S. neglecta*, *S. oceania*, and *S. robusta* (Angeles Alvariño, fishery biologist, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, pers. comm., April 1981).

†† Miscellaneous forms taken in low numbers included hydromedusae, siphonophores, syphozoans, heteropods, pteropods, cephalopods, cladocerans, monstrilloid copepods, stomatopod larvae, hyperiid amphipods, pleuteus larvae, thaliaceans, and ascidian larvae.

TABLE 2

Copepods Collected Above the Lagoon Shelf in Daylight with Nets of Different Mesh Size*

	0.333 MESH $N = 2$		0.165 MESH[†] $N = 2$	
TAXA	MEAN NO.	SIZE RANGE (MEAN)	MEAN NO. (ADJUSTED)	SIZE RANGE (MEAN)
Calanoids[‡]	17	0.7–1.3 (1.0)	310.0	0.3–1.0 (0.6)
Cyclopoids[§]	3	0.6–0.8 (0.7)	914.5	0.3–0.8 (0.4)
Harpacticoids[¶]	4	0.5–0.9 (0.6)	294.5	0.3–0.6 (0.4)

[*] Paired collections close to Station B during midafternoon, one with 0.333-mm mesh net in a 0.78-m^2 square frame, the other with a 0.165-mm mesh net in a 0.5-m circular frame. To make collections with the two net sizes equivalent, values given for the finer mesh are collected values times 3.1.

[†] Two additional collections with the finer mesh near Station A produced similar results but were not paired with the larger mesh and thus are not included here.

[‡] *Acartia negligens* and unidentified forms.

[§] *Corycaeus* sp. and *Oithona* sp.

[¶] *Tegastes* sp., *Metis holothuriae*, and unidentified forms.

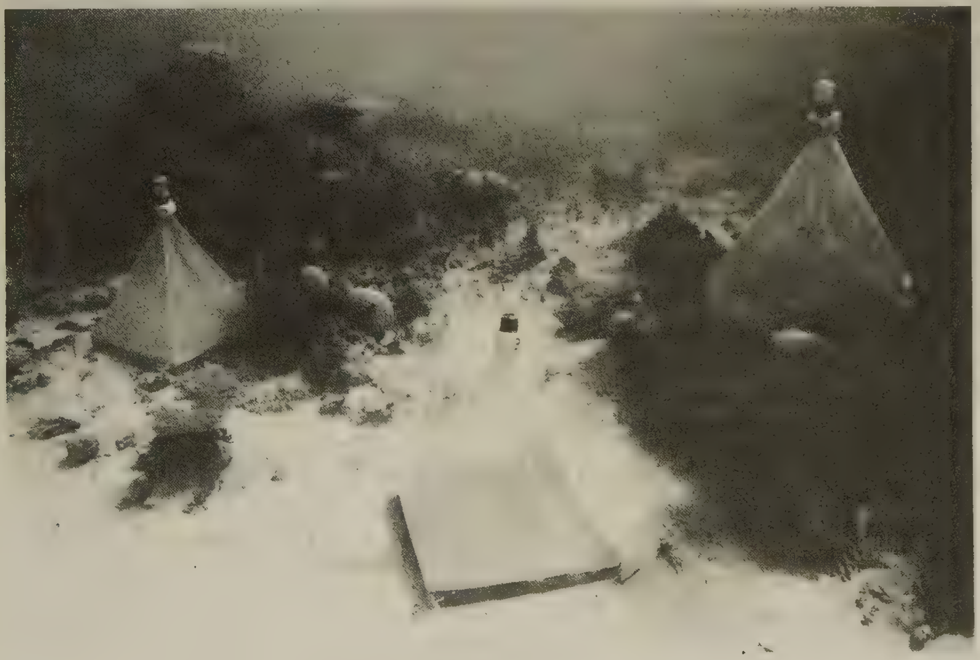

Figure 2. Typical arrangement of the traps used to sample meroplankters that rise into the water column from the major substrata on the lagoon shelf at Enewetak Atoll. Left to right: rubble, sand, and reef.

Both diurnal and nocturnal conditions were sampled. Each daytime deployment of the three traps was paired with a deployment that sampled the same spots during the preceding or following night. Some of the day/night pairs of sets began with daytime collections, others with the nighttime collections. When starting with the daytime collections, we placed the traps in position between sunrise and 0800 hr and retrieved the nets between 1730 hr and sunset, leaving the bases in place. Upon retrieval, all materials were washed and then removed for preservation in 4% formaldehyde (as were all our plankton collections). The nets, with empty cod ends in place, were then reattached to the bases and left in place throughout the night. The following morning, again between sunrise and 0800 hr, the entire traps—nets and bases—were retrieved and the collected organisms preserved as before. This sequence was reversed when we had begun the day/night pair of sets with the night collection. After completing one pair of sets, we moved to a different location and repeated the procedure for the next pair of sets. Six paired sets were made in the vicinity of Station B. Of the six near Station A, four were made in locations periodically swept by currents and two were made in nearby waters sheltered from these currents. In all, 56 samples were taken. (Four reef collections were canceled—two day and two night—while that trap was repaired.) The trap collections were made during the same periods as were the water-column collections, described above, and thus encompassed the same range of tides (spring to neap) and lunar phases.

Our trap collections (Table 3) showed that organisms which entered the water column from the benthos did so primarily at night (Wilcoxon two-sample test: $Z = -6.28$, $p < 0.0001$). These benthos-related forms, including various polychaetes, ostracods, mysids, tanaids, isopods, amphipods, and carideans, have been variously referred to as demersal plankton (Alldredge and King 1977, 1980; Porter and Porter 1977), epibenthic plankton (McWilliam et al. 1981), and meroplankton (Williams and Bynum 1972; Hobson and Chess 1979; Robichaux et al. 1981). We consider the relatively few organisms trapped by day to be of uncertain, or at most minor, significance.

Generally, the organisms that entered the water column at night were more numerous in the trap collections from areas sheltered from currents. The 18 trap collections made at night in areas sheltered from currents took $\bar{x} = 635.9$ (SE 163.3) individuals of 93 taxa, whereas the ten trap collections made at night where intermittent currents flowed took $\bar{x} = 360.4$ (SE 82.7) of 69 taxa. Although this difference lacked significance (Wilcoxon two-sample test: $Z = -0.79$, $p = 0.215$), certain groups were far more numerous in the sheltered area. This was particularly true of mysidaceans ($\bar{x} = 106.7$; SE 57.7) in collections from the sheltered area, compared to $\bar{x} = 3.5$ (SE 1.8) from the current area (Wilcoxon two-sample test: $Z = -3.15$, $p < 0.001$). Although these data document a general trend, they are insufficient to relate the benthic shelter sites of particular species to the current patterns.

Although our samples lacked the sensitivity needed to define specific benthic microhabitats of the three broad categories sampled—reef, rubble, and sand—the largest numbers came from the reef. The eight collections made at night on reef substrata took $\bar{x} = 935.13$ (SE 315.9) individuals of 76 taxa compared to $\bar{x} = 643.9$ (SE 72.3) of 79 taxa in ten collections from rubble and $\bar{x} = 113.1$ (SE 16.6) of 59 taxa in ten collections from sand.

Our scheduled collections did not include samples of the mysids that we observed swarming at many places on the shelf during the day, especially in areas sheltered from currents. These aggregations occurred as dense balls close to patch reefs and as immense mats 50 to 100 cm thick close above open sand. (An unscheduled pass with our 0.333-mm mesh net through a small segment of one such aggregation netted approximately 60,000 individuals, all *Anisomysis* sp., 1.5 to 4 mm long.) At the same time, much smaller aggregations of mysids, generally consisting of larger individuals, frequently occurred close beneath the water's surface. (An unscheduled pass with our net through one such relatively small aggregation enveloped the entire group, capturing approximately 1900 individuals, 6 to 7 mm long, again all *Anisomysis*

TABLE 3

ORGANISMS COLLECTED IN THE BENTHIC TRAPS ON THE LAGOON SHELF AT ENEWETAK ATOLL, DAY AND NIGHT

	DAY			NIGHT		
TAXA	% OCCUR.	MEAN NO.	(SE)	% OCCUR.	MEAN NO.	(SE)
Foraminiferans	71	9.96	(2.99)	96	35.32	(8.80)
Tretomphalus sp.	68	8.04	(2.72)	93	16.57	(5.60)
Cymbaloporella sp.	25	1.50	(0.64)	61	15.61	(4.33)
Others (undet.)	18	0.43	(0.20)	61	3.14	(0.66)
Polychaetes	25	0.25	(0.08)	82	2.50	(0.38)
Opheliids	7	0.07	(0.05)	43	0.89	(0.27)
Others	18	0.18	(0.07)	71	1.61	(0.29)
Gastropods	25	4.21	(3.63)	96	6.25	(1.27)
Ostracods	4	0.11	(0.11)	86	4.43	(0.89)
Myodocopids	4	0.07	(0.07)	71	3.64	(0.93)
Podocopids	4	0.04	(0.04)	36	0.79	(0.28)
Calanoids	54	1.61	(0.74)	89	5.43	(1.03)
Paramisophria sp.	—	—	—	46	1.54	(0.42)
Others	54	1.61	(0.74)	79	3.89	(0.86)
Cyclopoids	7	0.14	(0.10)	25	0.36	(0.14)
Harpacticoids	61	1.64	(0.46)	100	42.5	(13.14)
Peltidiids	32	0.50	(0.16)	79	20.68	(6.85)
Tegastids	—	—	—	11	2.11	(1.93)
Others	50	1.14	(0.35)	96	19.71	(5.53)
Mysidaceans	—	—	—	82	69.82	(37.71)
Pseudanchialina inermis	—	—	—	46	1.93	(0.53)
Siriella spp.	—	—	—	21	1.14	(0.76)
Gastrosaccus bengalensis	—	—	—	29	0.64	(0.24)
Other adults	—	—	—	14	0.86	(0.65)
Juveniles	—	—	—	57	64.96	(37.25)
Cumaceans	—	—	—	89	5.46	(1.20)
Tanaidaceans	21	0.50	(0.23)	79	7.50	(1.95)
Leptochelia spp.	14	0.39	(0.23)	75	6.46	(1.60)
Tanais sp.	4	0.04	(0.04)	18	0.86	(0.47)
Others	4	0.07	(0.07)	18	0.18	(0.07)
Isopods	4	0.07	(0.07)	89	6.86	(1.24)
Epicaridean larvae	—	—	—	43	1.43	(0.28)
Gnathiid females and juveniles	—	—	—	54	3.68	(0.93)
Others	4	0.07	(0.07)	71	2.04	(0.42)
Gammarideans	25	0.25	(0.08)	96	13.54	(2.05)
Synopia variabilis	—	—	—	39	2.29	(0.89)
Maera spp.	4	0.04	(0.04)	36	0.68	(0.25)
Elasmopus sp.	—	—	—	18	0.50	(0.28)
Aorids	—	—	—	57	3.93	(1.39)
Amphilochids	—	—	—	11	0.18	(0.12)
Others	21	0.21	(0.08)	82	5.96	(1.02)
Natantians	32	0.79	(0.40)	100	225.47	(51.67)
Larvae	32	0.79	(0.40)	86	213.39	(51.96)
Alpheids	—	—	—	64	2.93	(0.84)
Other carideans	—	—	—	96	9.04	(1.24)
Penaeids	—	—	—	4	0.11	(0.11)
Reptantians	7	0.07	(0.05)	68	78.14	(36.69)
Zoeae	7	0.07	(0.05)	43	76.96	(36.65)
Megalopae	—	—	—	43	0.93	(0.26)
Others	—	—	—	21	0.25	(0.10)

TABLE 3 (*Continued*)

	DAY			NIGHT		
TAXA	% OCCUR.	MEAN NO.	(SE)	% OCCUR.	MEAN NO.	(SE)
Chaetognaths	—	—	—	50	1.61	(0.45)
Spadella legazpichessi	—	—	—	32	0.68	(0.26)
Others	—	—	—	32	0.93	(0.37)
Fish eggs	57	2.43	(0.56)	93	27.46	(6.13)
Fish larvae	—	—	—	32	2.54	(2.13)
Fishes, postlarvae*	—	—	—	25	0.36	(0.14)
Miscellaneous	39	0.61	(0.18)	71	2.00	(0.36)
Total mean number		22.64			537.54	

* Includes *Amphioxus*.

sp.) These aggregations dispersed at nightfall and reformed the following morning.

ZOOPLANKTON FROM THE OPEN SEA

The zooplankton that arrived above the shelf from the open sea outside the atoll were sampled from the flow of water that crossed the interisland reef at high tide (Station C, Figure 1). To make these collections, we used the same net as at the other stations, but here we mounted it alongside a skiff anchored on an inflowing current near its maximum flow. During the collections the water was about 1.5 m deep and was moving 45 to 84 cm/sec^{-1} (determined by a current meter), so the net, positioned just beneath the surface, sampled most of the water column. We varied the time the net was in the water—4.75 to 7.50 min—according to the water flow, so that the volume of water filtered approximated that filtered by each of the regular 10-min diver-controlled collections at the other sites. Because we had found earlier that nearshore zooplankters were most numerous in the water column on dark nights (Hobson and Chess 1976), our nocturnal collections were made during the new moon.

Each collection on the interisland reef at Station C was followed within 30 min by another collection directly downcurrent above the lagoon shelf. This second collection, made using the standard diver-controlled method, provided a basis for inferring the origin of certain zooplankters above the lagoon shelf. We reasoned that species which were more numerous in the cross-reef flow than above the shelf downcurrent were likely to be transients from outside the lagoon. (We expected that zooplankters in the shallow water crossing the reef would quickly disperse upon entering the deeper water behind the reef.) On the other hand, species that were few or absent in the waters coming into the lagoon, but numerous above the shelf directly downcurrent, were likely to be residents of the shelf or to have come from offshore in the lagoon.

The number of zooplankters carried over the reef from outside the atoll was much greater at night (Table 4), which was consistent with the nocturnal increase in numbers of zooplankton above the shelf. The nighttime flow carried $\bar{x} = 8208$ zooplankters compared to $\bar{x} = 460$ in the daytime flow (omitting the foraminiferan *Discorbis* sp.; see Table 1, footnote 2). Hence we concentrate on organisms arriving at night. Zooplankters that were numerous in the nocturnal reeftop flow, but which were at the same time considerably fewer above the shelf downcurrent (indicating a probable origin outside the atoll), included halocyprid ostracods, the calanoid *Undinula vulgaris*, the euphausid *Pseudeuphausia latifrons*, certain of the chaetognaths (which were not identified to species but probably included those listed in Table 1, footnote 7), and certain larvae, including natantians and zoeae. In comparison, zooplankters few or absent in the nocturnal reeftop flow, but at the same time

TABLE 4

Zooplankters in Currents Crossing the Interisland Reef Compared to Downstream on the Lagoon Shelf[*]

	DAY				NIGHT			
	REEFTOP $N = 2$		LAGOON SHELF $N = 2$		REEFTOP $N = 2$		LAGOON SHELF $N = 2$	
TAXA	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.
Foraminiferans	100	630.0	100	59.5	100	80.0	100	322.5
Tretomphalus sp.	100	66.5	100	37.0	100	54.5	100	215.0
Discorbis sp.	100	563.5	50	21.5	100	20.5	100	100.5
Cymbaloporella sp.	—	—	25	0.5	50	2.0	50	2.0
Globigerina sp.	—	—	50	0.5	50	1.5	50	4.0
Others	—	—	—	—	50	1.5	50	1.0
Siphonophores	—	—	50	0.5	50	1.5	50	8.0
Polychaetes	100	2.0	—	—	100	6.5	100	3.0
Opheliids	50	1.0	—	—	—	—	100	3.0
Nereid epitokes	—	—	—	—	100	5.0	—	—
Tomopteris sp.	—	—	—	—	50	1.5	—	—
Undetermined	50	1.0	—	—	—	—	—	—
Veligers	100	36.0	100	60.0	100	20.0	100	11.0
Ostracods	50	0.5	50	0.5	100	124.0	100	61.0
Cypridinaceans	50	0.5	50	0.5	50	2.0	100	49.0
Halocyprids	—	—	—	—	100	122.0	100	12.0
Calanoids	100	43.5	100	70.0	100	3592.5	100	1457.5
Acartia negligens	100	8.0	100	33.0	100	110.0	100	10.0
Undinula vulgaris	100	10.5	—	—	100	2605.0	100	1000.0
Calanopia minor	—	—	—	—	—	—	50	3.0
Lucicutia flavicornis	—	—	—	—	100	216.0	100	25.0
Ten others[†]	50	6.0	50	0.5	100	91.5	100	49.5
Undetermined	100	19.0	100	36.5	100	570.0	100	370.0
Cyclopoids	100	10.0	50	30.5	100	55.0	50	14.0
Corycaeus sp.	50	1.0	50	24.0	100	34.0	50	10.0
Oncaea sp.	100	8.5	50	6.0	—	—	—	—
Oithona sp.	—	—	—	—	50	15.0	50	4.0
Sapphirina sp.	50	0.5	50	0.5	50	4.0	—	—
Copilia sp.	—	—	—	—	50	2.0	—	—
Harpacticoids	100	8.0	50	2.5	50	4.0	100	34.0
Peltidiids	—	—	50	0.5	—	—	—	—
Metis holothuriae	—	—	50	2.0	—	—	—	—
Tegastids	—	—	—	—	50	4.0	50	4.0
Undetermined	100	8.0	—	—	—	—	100	30.0
Mysidaceans	50	4.0	100	185.0	50	4.0	100	2026.0
Anisomysis spp.	—	—	50	10.0	—	—	100	220.0
Pseudanchialina inermis	—	—	—	—	50	4.0	100	36.0
Gastrosaccus bengalensis	—	—	—	—	—	—	50	30.0
Juveniles	50	4.0	100	175.0	—	—	100	1740.0
Stomatopod larvae	—	—	—	—	100	420.0	100	118.0
Cumaceans	—	—	—	—	—	—	100	12.0
Tanaidaceans	100	5.0	50	3.5	—	—	100	16.0
Leptochelia sp.	100	5.0	50	2.0	—	—	100	8.0
Tanais sp.	—	—	50	1.5	—	—	50	8.0
Isopods	50	10.0	—	—	—	—	50	0.5
Epicaridean larvae	50	10.0	—	—	—	—	50	0.5
Gnathiid females and juveniles	—	—	—	—	—	—	—	—

TABLE 4 (*Continued*)

	DAY				NIGHT			
	REEFTOP $N = 2$		LAGOON SHELF $N = 2$		REEFTOP $N = 2$		LAGOON SHELF $N = 2$	
TAXA	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.
Gammarideans	50	1.5	100	2.0	100	6.0	100	33.0
Synopia variabilis	—	—	—	—	50	2.0	100	14.0
Maera sp.	50	1.0	—	—	50	2.0	100	1.0
Four others‡	50	0.5	50	1.0	—	—	100	4.0
Undetermined	—	—	50	1.0	50	2.0	100	14.0
Euphausiids	—	—	—	—	100	640.0	100	48.0
Pseudeuphausia latifrons	—	—	—	—	100	640.0	100	48.0
Natantian larvae	100	10.0	100	9.0	100	420.0	100	320.0
Natantian postlarvae	50	4.0	—	—	100	72.0	100	115.0
Ogyrides sp.	—	—	—	—	50	0.5	—	—
Alpheids	50	4.0	—	—	—	—	50	16.0
Other carideans	—	—	—	—	100	39.5	100	95.0
Lucifer sp.	—	—	—	—	100	32.0	50	4.0
Zoeae	100	44.0	100	33.0	100	1110.0	100	180.0
Megalopae	—	—	—	—	100	40.0	100	40.0
Chaetognaths	50	12.0	100	21.0	100	720.0	100	290.0
Larvaceans	—	—	50	1.5	50	24.0	50	4.0
Fish eggs	100	175.0	100	50.0	100	6200.0	100	230.0
Fish larvae	—	—	50	0.5	100	22.0	100	32.0
Miscellaneous§	—	—	—	3.5	—	86.7	—	4.6

* Includes taxa where mean number of individuals at either station, day or night, was greater than 1.0.

† Other calanoids included (* = reeftop; + = lagoon shelf): *Candacia* sp.*+, *Centropages* sp.+, *Euchaeta marina**+, *Labidocera laevidentata*+, *Pleuromamma abdominalis**+, *P. xiphias**+, *Pontillina morii*+, *P. plumata*+, *Tortanus* sp.*+, and *Undinula darwini*.

‡ Other gammarideans included: *Leucothoe hyhelia*; *Prodocerus* sp.; an amphilochid (nighttime lagoon shelf); and *Seba* sp. (one individual, daytime, reeftop; not previously reported from Micronesia).

§ Miscellaneous forms taken in low numbers included pteropods, cephalopods, cladocerans, cypris larvae, stomatopod larvae, hyperiids, insect (*Holobates* sp.), pluteus larvae, thaliaceans, and ascidian larvae.

abundant above the shelf downcurrent (indicating they had not arrived from outside the lagoon), included cypridinacean ostracods, mysidaceans, cumaceans, tanaids, and gammarideans. Significantly, these were species known from our benthic trap collections (Table 3) to include residents of the shelf that shelter on the substrate during the day.

ZOOPLANKTON FROM THE DEEPER WATER OF THE LAGOON

Probably zooplankters that moved over the lagoon shelf at night from the deeper waters of the lagoon advanced over a broad front. Presumably this was not a purposeful shelfward migration, but rather a net movement in that direction by some proportion of the population. We would expect it to be a result of dispersing in the surface waters after an ascent from the depths adjacent to the shelf. Although such an advance would be highly diffuse, and not directly measurable by our collecting methods, it seemed possible to develop inferential evidence that would identify some of the prominent organisms involved.

Having determined that the larger transients are above the shelf only at night, we reasoned that those from the deep lagoon would be numerous there during the day. To identify them, we established Station D about 1 km beyond the outer edge of the shelf, where the water was about 30 m deep. This site was selected after visual search, and random sampling, had determined that larger zooplankters were concentrated between depths of

9 and 15 m but were sparse or absent both above and below these depths. To sample, we pushed the same net used at the other stations along a course that led up and down through the depths where the zooplankters were concentrated. As a check on our visual impression that this concentration did not extend deeper (where zooplankters would be increasingly difficult to see), we then made a second collection 10 m below the first. Two weeks later we went directly to the same location, immediately found the concentrations at the same level as before, and repeated the collections.

Of species that were numerous above the lagoon shelf at night, but virtually absent in collections there by day (Table 1), only the calanoid *Undinula vulgaris* and chaetognaths were numerous in the daytime collections at Station D. These, however, were the richest taxa in those collections (other than various larval forms). The two collections (2 weeks apart) that sampled the concentration of zooplankters between depths of 10 and 15 m took 370 and 310 *Undinula vulgaris* (2–3 mm) and 240 and 840 chaetognaths (4–14 mm). *Undinula vulgaris* represented 14.9%, and chaetognaths 23.8%, of the nonlarvae in the two collections. On the other hand, neither *U. vulgaris* nor chaetognaths occurred in the two collections made 10 m deeper at the same time and place.

But even if we can assume that *U. vulgaris* and chaetognaths from the deep lagoon were among the transients above the shelf at night, there remained the problem of distinguishing them in the shelf zooplankton from others of the same species that, as determined from our collections above the interisland reef (Station C: Table 4), came from the open sea. This distinction is considered in the following discussion.

DISCUSSION

Although many zooplankters of about 1 mm or less were numerous above patch reefs on the lagoon shelf during both day and night, it was evident that the vast majority of those larger than about 1.5 mm were in the water column there only at night. Many of these larger individuals were shelf residents that by day were in or on shelf substrata, or in swarms close above these substrata, whereas others were transients from the open sea or from the deep lagoon. Here we make further distinctions between the residents and transients, while discussing how their ascent in the water column represented a general nocturnal vertical migration with subsequent dispersion in the surface waters. We also discuss how the resulting distribution was influenced by water currents. First, however, possible sources of sampling error are acknowledged.

Possible Sampling Error

Because our plankton collections were from relatively shallow water, some may have included strictly benthic forms that had been swept into the water column by turbulence, perhaps attached to algal fragments (for example, the foraminiferan *Discorbis* sp.). This contamination would most likely occur in our traps or when our plankton nets sampled close to the sea floor, but we believe that it had little or no effect on our conclusions. Drifting plant fragments were far more abundant by day (Table 1), for example, and the zooplankters upon which we base our analysis were consistently more numerous in our collections at night. Probably some strictly benthic forms climbed the inner sides of our traps and entered the collections (Hobson and Chess 1979; Robichaux et al. 1981), but these would not include organisms important to our analysis, which were also taken in the water column by our plankton nets. Furthermore, confidence in our data is increased by the consistency of results from these two different collection methods—nets and traps—combined with direct observations of many of the organisms *in situ*.

Shelf Residents Among the Larger Zooplankters

Certain zooplankters above the shelf at night were identified as residents when captured by our traps as they emerged from shelf substrata. Prominent among them were various polychaetes, ostracods, mysids, tanaids, isopods, amphipods, and carideans. Possibly some individuals of these species also came from benthic habitats in deeper parts of the lagoon, but there was no evidence in the samples from the reeftop flow (Station C) that any came from outside the atoll.

The residents also included those species that aggregate by day in dense swarms close to benthic substrata. Although at Enewetak we noted this behavior only among mysids, especially *Anisomysis* spp., we have seen it among copepods elsewhere (Hobson and Chess 1979 and unpublished data). Daytime swarms of both mysids and copepods are widespread in tropical reef communities (Emery 1968; Hamner and Carleton 1979).

Probably the residents also included *Calanopia minor*, although the diel distribution of this calanoid remains somewhat uncertain. It was the most numerous copepod in nocturnal collections above that part of the shelf sheltered from currents, but was much scarcer where intermittent currents flowed and, with the exception of just a single individual, was not taken by us during the day (Table 1). It has been reported that many individuals of this species spend the day in the sediments of the Enewetak Lagoon (Barnett 1967), as is the case with a congener, *C. americana*, at Bermuda (Clarke 1934). So even though we failed to collect *C. minor* in our benthic traps, we nonetheless believe that at least many of those above the shelf at night are in the shelf sediments by day and therefore are residents of that habitat. Many of those we collected were taken at about last evening light—the same time that many known residents first appear in the water column—so these could not have come from far away, especially as the currents that might have accelerated an arrival from greater distances were lacking where they were most abundant. Some *C. minor* may have arrived above the shelf at night from the deeper waters of the lagoon—Barnett (1967) found this species abundant at the base of the water column in the mid-lagoon during the day. But there is no evidence that any come from the open sea, as none were among the zooplankton arriving in the reeftop flow. Similarly, a congener, *C. elliptica*, was the major calanoid collected by Sale et al. (1976) in a lagoon of the Great Barrier Reef, Australia, but was not among the calanoids they collected in open water outside that lagoon. And in collections by Clarke (1934) at Bermuda, *C. americana* was the dominant copepod in bays and harbors but was absent in collections from the ocean outside (except in sharply decreasing numbers close to the mouths of the enclosed waters).

EFFECTS OF CURRENTS: Certainly the resident zooplankters would benefit from means to prevent being carried away from their home grounds by water currents. To consider the vulnerability of the residents to currents, however, requires a measure of their swimming abilities. This measure is lacking for the species considered here, but rough approximations can be based on swimming speeds of comparable species measured elsewhere. Of mysids, which included perhaps the strongest swimmers among the zooplankters considered here, those species that have been studied traveled up to about 15 cm/sec^{-1} (Steven 1961; Clutter 1969). Because this would not be enough to overcome even the relatively weak currents (up to 25 cm/sec^{-1}) that regularly flowed through our study area, we would expect the current patterns to have a strong influence on the distribution of these zooplankters.

Those residents that are benthonic during part of the diel cycle—including harpacticoids, mysidaceans, cumaceans, tanaids, isopods, and gammarideans—probably have close ties to specific benthic habitats and avoid currents that would carry them away. Certainly the nocturnal distribution of *Calanopia minor* indicated that it favored areas of reduced current. But when all those collected by our benthic traps are considered (Table 3), the numbers collected were not significantly greater in the sheltered area than in the current area. Apparently, many with ties to benthic habitats tolerated these weak currents, perhaps by taking advantage of eddies or by limiting their planktonic modes to periods of slack water. We suspect, however, that they would have been less successful adjusting to conditions where currents were much stronger and, in fact, they were sparsely distributed where currents exceeding 1 m/sec^{-1} flow into the lagoon through the deeper channels (Hobson and Chess 1978). Further evidence that these forms do, in fact, avoid currents exists in their absence in the reeftop flow (Table 4). Considering their prominence in the nocturnal plankton above the shelf (Table 1, 3, and 4), there must have been at least some representatives of these taxa in the nocturnal plankton above reefs outside the lagoon. Although we would expect them to be considerably fewer in that surge-swept habitat than in the lagoon, some should have been carried in the reeftop flow—unless they avoided this current. Significantly, many larvae of these same taxa, including zoeae, megalopae, and natantian larvae, were numerous in the nocturnal reeftop flow (Table 4) and clearly did not avoid this current. At least many of these larvae are benthonic by day (Table 3), but unlike their adults they apparently lacked close ties to specific benthic habitats. In fact, probably at least many of them benefited from currents as adaptive means to disperse.

Those resident mysids that swarmed close to the shelf floor during the day were numerous only in areas sheltered from currents. All seemed to be *Anisomysis* spp., and members of this genus were not among the mysids that sheltered in or on the substrate (Table 3). Apparently, therefore, these species do not have the capacity to avoid intermittent currents by sheltering there. The relatively few mysid swarms that occurred in areas of intermittent current were sheltered in the lee of patch reefs when these currents flowed (Hobson and Chess 1978).

Other resident zooplankters that have been reported to swarm close to benthic substrata by day—including certain cyclopoids such as *Oithona* spp. and calanoids, such as *Acartia* spp. (Emery 1968; Hamner and Carleton 1979; Hobson and Chess 1979)—may similarly avoid currents. Although the reports cited did not consider the distributions of these species relative to currents, they did contain evidence that currents are avoided. For example, there is frequent mention of copepod swarms being in such places as "between coral heads or other sheltered locations" (Emery 1968:295) and "most pronounced . . . in sheltered embayments" (Hamner and Carleton 1979). Similarly, when Hamner and Carleton once saw copepods in small swarms on a windward reef slope, they considered them to be in an unusual location. They also considered it noteworthy that in one place where a 5 cm/sec^{-1} current flowed, small swarms of *Acartia* maintained station in eddies downcurrent of boulders.

Transients Above the Lagoon Shelf at Night

In considering as transients those species that appeared above the shelf from the ocean outside the atoll, or from the deeper waters of the lagoon, we are mostly concerned with holoplankters that perform diel vertical migrations in open water. The arrival of these species in the shallows at night appears related to a general ascent into the surface waters after dark, a phenomenon widespread among the zooplankters of Pacific atolls (Johnson 1949; Hobson and Chess 1973), as it is among zooplankton in general (Cushing 1951). Presumably many of the zooplankters that rise into surface water from open-ocean depths windward and upcurrent of the atoll are carried into the lagoon when these waters wash over the interisland reef. And many of the zooplankters that disperse into the surface waters from lagoon depths would be expected to spread over the adjacent shelf unless blocked by currents from that direction (Hobson and Chess 1978).

The major transient zooplankter above the lagoon shelf was the calanoid *Undinula vulgaris*. This species was the most widespread and generally abundant zooplankter in that habitat at night, but it was sparsely distributed there during the day (Table 1). *Undinula vulgaris* has been considered a lagoon endemic that only incidentally occurs in the open sea (Johnson 1949), but while we found it a major species among the deep-lagoon zooplankters during the day, its numbers in water that flowed into the lagoon from outside the atoll at night (Table 4) indicate that it also was abundant in the surrounding ocean. Reports from other areas support this view. For example, in the plankton collections made by Sale et al. (1976) inside and outside a lagoon on the Barrier Reef, *U. vulgaris* was a major species only in the collections from outside. And while this widely ranging species is known to have neritic tendencies (Grice 1961) and was not among the calanoids collected by Chiba et al. (1955) at oceanic stations in the Micronesia area, it has been found far from land (Owre and Foyo 1967). Furthermore, in their daytime collections at Enewetak, Gerber and Marshall (1974:816) found the shallows above the lagoon shelf (including a station near our study site) "largely devoid of *U. vulgaris*," when at the same time they collected it abundantly in the mid-lagoon and in a deep passage from the sea. So whether in the lagoon or in the surrounding ocean, *U. vulgaris* seems to be a species of deeper water rather than the nearshore shallows.

EFFECT OF CURRENTS: The transient zooplankters, unlike the residents, did not show adaptive behavior related specifically to the currents that flowed over the shelf. Perhaps this should been expected, because it seems unlikely that these open-water species would have acquired adaptive responses to characteristics of shallow-water habitats. Instead, the currents appeared to influence them simply by accelerating their movements downstream and blocking their movements upstream. This apparently straightforward relationship between their movements and current provides means to judge whether certain open-water transients that occurred above the shelf during the night were likely to have come from the open sea or from the deeper waters of the lagoon.

Our consideration of this point is highly conjectural, but it illustrates some of the variables that should influence the distribution of transient zooplankters above the shelf. The analysis is limited to *U. vulgaris*, which would seem the best choice to represent the variety of transients above the shelf after dark. Among the many open-sea species prominent in the reeftop flow (Table 4), only *U. vulgaris* was identified as abundant and widespread above the shelf. And of the species that were abundant above the shelf at night, but much fewer there during the day (Table 1), only *U. vulgaris* was identified as numerous at our daytime collecting site offshore in the lagoon (Station D). Chaetognaths seemed to have a similar pattern of occurrence, but the six or more species in our samples (Table 1, footnote 7) were not distinguished in the individual collections.

To determine which of the many *U. vulgaris* above the shelf at night came from the open sea, and which were more likely to have come from the deep lagoon, we assumed they would have arrived from those opposite directions in numbers relative to differing conditions of tide, current, and time of night. We reasoned that individuals from each of the two directions could be distinguished by collections that sampled a diverse combination of these variables. Thus certain of the collections at Stations A and B sampled on the higher tides, when currents flowing across the interisland reef should have carried zooplankters from outside the atoll but blocked the shelfward advance of zooplankters from the deeper waters of the lagoon. And certain other collections sampled the lower tides, when the exposed interisland reef blocked the flow of water and the zooplankters from outside the atoll, but when, in the absence of this flow, the zooplankters from the deep lagoon should have been free to spread over the shelf. Obviously the length of time the condition had been in force should have been important. The time of night should have been important, too. While zooplankters from the open sea should have arrived shortly after sunset when the currents that carried them were flowing, zooplankters from offshore in the lagoon, being without assisted transport, could not have spread to the inner regions of the shelf until later during the night, even under the most favorable conditions.

The nocturnal occurrences of *U. vulgaris* above the shelf at Stations A and B showed a clear pattern (Table 5). The large number at Station A during high tide (collections A_2 and A_4) undoubtedly arrived in the currents that flowed across the interisland reef from the open sea at this time. Not only did these currents provide transport from that direction; they also blocked shelfward movements by zooplankters from the deep lagoon. On the other hand, because these currents were large-

TABLE 5

Numbers of *Undinula vulgaris* Collected at Night Under Varying Environmental Circumstances Above the Lagoon Shelf at Enewetak Atoll

	STATION A (INTERMITTENT CURRENT)						STATION B (NO CURRENT)					
	HIGH TIDE		LOW TIDE, EARLY		LOW TIDE, LATE		HIGH TIDE		LOW TIDE, EARLY		LOW TIDE, LATE	
SPECIES AND CONDITIONS	A2	A4	A1	A6	A3	A5	B2	B4	B1	B6	B3	B5
Species												
Undinula vulgaris	400	170	10	0	960	28	24	72	8	0	180	600
Conditions												
Date	5/30	6/4	5/27	6/4	6/2	6/4	5/30	6/4	5/27	6/4	6/2	6/4
Time[*]	0500	0130	2330	2115	0330	0445	0430	0100	2300	2045	0300	0415
Tide height[†]	3.7	3.2	1.1	2.2	2.3	2.5	3.5	3.3	1.2	2.2	2.3	2.6
Tide direction[‡]	F4.5	E1.1	E5.5	F2.0	F0.3	E4.2	F4.0	E0.5	E5.0	F1.5	E5.5	E3.8
Current (cm^{-1})	0[§]	15	8	0	0	10	0	0	0	0	0	0
Moon[¶]	0.29x	0.50x	0.07x	0.57p	0.43x	0.50x	0.29x	0.50x	0.07x	0.57p	0.43x	0.50x

[*] Sunrise on these dates was at 0653 hr; sunset at 1932–1934 hr (calculated from sunrise and sunset table, Tide Tables 1979, National Ocean Survey, NOAA, U.S. Dept. of Commerce).

[†] Values represent height of the tide (in feet) above mean lower low water, as calculated from Tide Tables 1979, Dept. of Commerce. During our 3 weeks at Enewetak mean high tide was 3.8; mean low tide was 1.5.

[‡] E = ebb tide; F = flood tide. Numeral is hours that tidal phase had been in effect (e.g., E5.5 = tide had been ebbing for 5.5 hr).

[§] Moderate current passing within 10 m of collection site. (See text for description of current patterns at this station.)

[¶] Numeral represents moon phase, where 0.00 = new moon and 1.00 = full moon; x = moon not visible during observations (owing to time of night or cloud cover); p = moon visible.

ly blocked at Station B, it is not surprising that there were relatively few *U. vulgaris* at this site during the same high tides (collections B_2 and B_4). Although the origin of these few remains uncertain, the lagoonward drift noted above the shelf offshore from this site during high tide would have been enough to prevent a shelfward advance by *U. vulgaris* from the deep lagoon. Although this drift was estimated as only a few cm/sec^{-1}, presumably this would have been too much for *U. vulgaris* to swim against. Although there are no data on the swimming capabilities of this species, individuals of another calanoid, *Metridia pacifica*, 2–3 mm long and therefore comparable in size to *U. vulgaris*, move 0.8 to 1.2 cm/sec^{-1}—and this is considered fast for a copepod (Enright 1977).

On the other hand, the *U. vulgaris* that were abundant at both Stations A and B during low tide late at night probably came from the deep lagoon (Table 5: low tide, late collections A_3, A_5, B_3, B_5), because at this time the currents that had carried zooplankters onto the shelf from the open sea during high tide were shut off by the exposed interisland reef. That so few were present at both stations during low tide earlier in the night (Table 5: low tide, early collections A_1, A_6, B_1, B_6) can be explained by the time they would have required to spread over the shelf after rising into the surface waters at nightfall—even those that rose out of the depths close to the shelf's edge. Being without benefit of the current that accelerated the movement of individuals from the open sea, it must have taken *U. vulgaris* and most others at least several hours to reach the inner regions of the shelf (based on the swimming speed of a similar species, cited above), and this would have been with a direct, purposeful advance, which seems unlikely to have occurred. More likely it took them considerably longer.

The relatively low numbers of *U. vulgaris* in collection A_5 despite the late hour may relate to the 10 cm/sec^{-1} current that was running against their advance at the time (Table 5: low late tide); as noted in the Methods section, even during low tide the trade winds or seas sometimes drove enough water across the interisland reef to generate currents on the shelf. The relatively few *U. vulgaris* in this collection certainly did not swim against a 10 cm/sec^{-1} current, but they may have arrived above the shelf before the current gained strength or may have benefited from a nearby eddy. Also, they may have been carried in wind-driven water that crossed the reef from the open sea at low tide, or among others that entered the lagoon from the open sea during high tide earlier that night.

Possibly the increased numbers of *U. vulgaris* during late low water represented an accumulation of individuals that had been carried into the lagoon from the open sea during high water earlier that night. But this would not explain the comparatively low numbers collected at the sheltered site during late high water (when conditions for an arrival from seaward would seem more favorable). In our opinion, the combination of data and circumstances arrayed in Table 5 is best explained if, in the absence of currents at night, large numbers of zooplankters from offshore in the lagoon spread over the lagoon shelf.

The Larger Zooplankters at Dawn

The routes taken by the larger zooplankters to arrive above the shelf at night seem reasonably clear. But what happened to them at dawn? Those residents with close ties to benthic substrata would have had no problem returning to their benthic habitats if, as it appears, they were able to stay above these habitats during their noctural excursions into the water column. But what about *U. vulgaris* and other transients that arrived from the open sea or the deeper waters of the lagoon? Certainly there was no return for them over the interisland reef to the open sea. Where the lagoonward currents flowed, as at the exposed site (Station A), many, if not most, may have been carried off the shelf into the deep lagoon before dawn. But in the absence of such currents, as at the sheltered site (Station B), we would expect at least many to have been stranded above the shelf at daybreak. It seems unlikely that they migrated across the shelf before descending into the depths beyond the dropoff, because in their normal deep-water habitat the appropriate behavior at daybreak for most is a direct descent. Possibly they descended directly to the shelf floor to become mixed and unrecognized in the detritus that accumulated on the sand. It seems more likely, however, that with daybreak in these unfamiliar shallows at least many of the open-sea zooplankters became increasingly vulnerable to planktivorous fishes and were consumed. Although *U. vulgaris* was scarce in the diurnal plankton collections made above the shelf (Table 1), the earliest of these collections was made at 1030 hr, and by that time many could have been removed by diurnal planktivores. Significantly, 2–3-mm individuals of this species were the major prey of the diurnal planktivore *Chromis carulea* at the sheltered site during midday (Hobson and Chess, unpublished data).

Thus the experience of open-water transients that occur above the lagoon shelf at night would seem much like that suggested for vertically migrating oceanic zooplankters that reportedly are carried above coastal shelves during their nocturnal occurrences in the surface waters. The reports suggest that these zooplankters risk being trapped by the seafloor in these coastal shallows during attempts to regain their normal daytime depths, and that this situation renders them vulnerable to predators (Isaacs and Schwartzlose 1965; Pereyra et al. 1969; Clarke 1984).

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Relationships among fishes and their prey in a nearshore sand community off southern California

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Synopsis

Trophic relationships among marine fishes in a nearshore sand environment off southern California showed that the species were distinguished by specific morphological and behavioral features adapted to capture the prey, and evade the predators, that were characteristic of that habitat. Species that foraged primarily by day included the serranid *Paralabrax clathratus*, the embiotocid *Embiotoca jacksoni*, and the labrids *Halichoeres semicinctus* and *Semicossyphus pulcher*. Primarily nocturnal foragers included the ophidiid *Chilara taylori*, the sciaenid *Umbrina roncador*, the embiotocids *Cymatogaster aggregata* and *Hyperprosopon argenteum*, and the pleuronectid *Pleuronichthys coenosus*. The bothid *Citharichthys stigmaeus* regularly fed during both day and night. The major predatory threat to these fishes came from the bothid *Paralichthys californicus*, which was primarily diurnal. In combination, these fishes possessed an array of behavioral and morphological feeding adaptations that closely matched the feeding opportunities present in that habitat. Not only did they consume, as a group, every species identified in samples of organisms from the environment (except the holoplankton, as discussed), they exploited these species over virtually the entire size ranges present. We infer from these circumstances that the species composition of fishes in this community was strongly influenced by the presence of specific feeding opportunities.

Introduction

Many distinctive features of nearshore marine fishes are adaptive because they provide means to capture prey or to thwart predators. This can be inferred from the morphology and behavior of species that interact as predator and prey, as determined by comprehensive studies of food habits (e.g. Hiatt & Strasburg 1960, Randall 1967), especially when the food habits are related to specific morphological features (e.g. Keast & Webb 1966), or to behavior (e.g. Hobson 1974). It follows, then, that interactions between predators and prey should be important forces in determining the species composition, and therefore the diversity, of marine fish communities.

There has been little attempt to study the influence of predator-prey interactions on the species composition of fishes in natural communities. It has been shown that purposeful or inadvertent introductions of exotic predators can alter the species composition in lakes, streams, or other enclosed bodies of water (e.g. Zaret & Paine 1973). And fishery managers have long recognized the potential of regulating prey populations in these habitats by manipulating predators (e.g. Swingle 1949). But these reports described relationships in closed ecosystems, where the interacting species were forced to contend with selection pressures outside their evolutionary experience. Until now there has been virtually no consideration of how trophic interactions might influence the species composition of fishes in an open marine system, although Stephens & Zerba (1981) suggested that an 'abundant food supply' was one of several factors contributing to the diversity of fishes on a reef in southern California.

This paper shows how the species composition of fishes over a nearshore sand bottom off southern California has been influenced by the need to capture the prey, and to avoid the predators, which are characteristic of that setting. Our account describes feeding behavior, illustrates relevant behavioral and morphological features, and recounts the array of organisms in the environment that represented potential prey.

Of the many studies of trophic relations in fishes, few have attempted to assess the potential food-base, and these few have limited their coverage to just parts of trophic systems, e.g. planktivores and zooplankton (Narver 1970, Hobson & Chess 1978), and other trophic guilds (e.g. Laur & Ebeling 1983). This lack of study reflects the difficulty in coordinating observations of feeding behavior, gut-content samples, and samples of potential prey in the environment. Even when the complex timing problems in sampling have been solved, there remains the highly difficult and time-consuming task of sorting and identifying the many organisms involved. To our knowledge, the present study is the most intensive account yet made of trophic relations among the fishes and other organisms living together in a natural marine habitat.

Methods

Study site

We studied a relatively simple system in an open-sand habitat in Ripper's Cove (Fig. 1), an embayment about 400 × 150 m in area, 9 km east of the Isthmus, on the northern shore of Santa Catalina Island (lat 33° 26′ N, long 118° 125′ W). The cove, bordered by a sand beach, was floored largely by sand under no more than 15 m of water. At both ends of the cove a rocky substrate forested by giant kelp, *Macrocystis pyrifera*, extended 10–20 m offshore.

The sampling centered around a 50 × 4 m tract established on open sand in 10 m of water, about 100 m from shore, and 50 m from the nearest rocks or kelp. The tract was marked by a fiberglass measuring tape placed only when counts or collections were being made, but an iron rod at each end of the line remained in place during the period of study. The fishes were observed throughout the cove, but specimens collected for gut-content analysis were taken over the open sand, within 20 m of the sampling tract defined above. All fish counts and all samples of organisms that represented the potential prey in the environment were taken in, and directly above, the sampling tract.

Sampling

To effectively relate the organisms taken as prey to the samples of organisms from the environment, we had to reduce the complicating variables associated with seasonal and lunar changes. So all samples were taken at quarter moon during one month, July. And because we knew that distinctive diurnal and nocturnal modes prevail in California nearshore fishes (e.g. Ebeling & Bray 1976), the collections were timed to avoid mixing representations of the two. Thus, fishes collected for gut-content analysis were taken either late in the afternoon, or during the 2 h immediately before first morning light (one exception, noted below) – a practice that has proven effective in distinguishing diurnal and nocturnal feeding among fishes in this region (Hobson & Chess 1976). The corresponding collections of potential prey organisms in the environment were made in the middle of the day (1100–1300 h), and middle of the preceding, or following night (2300–0100 h). We assumed these times were roughly midpoints in the feeding periods of the diurnal and nocturnal fishes, respectively.

Three comparable day/night series of collections, two weeks apart, were made: one at the beginning of the month, one in the middle, and one at the end. The nocturnal collections at the begin-

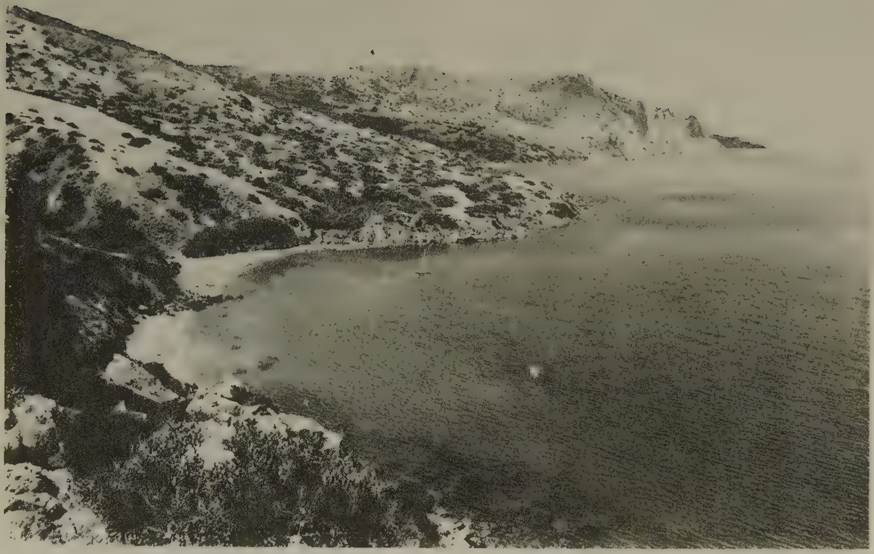


Fig. 1. Ripper's Cove, Santa Catalina Island, California.

ning and end of the month occurred just before last-quarter moonrise, whereas the nocturnal collections during mid-month occurred just after first-quarter moonset. So while the moon was below the horizon when the samples from the environment were taken, the fishes collected just before dawn on these dates presumably had experienced moonlight during some portion of their feeding periods. The number of samples that could be taken was limited by two constraints: (1) the tight coordination required between the collections of fishes for gut contents, and the collections of prey samples from the environment, and (2) the risk of disturbing this relatively simple system by removing too many of its components from so small an area over such a short time.

Although the data presented in this paper represent events and circumstances during just one month, our interpretations of these data benefit from over 3 yr of intensive study of the nearshore communities of Santa Catalina Island, and over 25 yr of experience with the southern California fauna.

Fishes

Each of the three collection series included both a diurnal and a nocturnal count of post-juvenile fishes seen during one transit of the sampling tract. An underwater light was used during the nocturnal counts. Although early juveniles often were present at night, we omitted them from the counts. This is because when juveniles first appear in benthic habitats they often occur where their behavior and morphology are irrelevant to local conditions (e.g. Hobson 1984), which makes them inappropriate for this study.

The fish specimens collected for gut contents, all taken with spears, were sampled at the specified times of day and night throughout the study period. Shortly after being collected, each specimen was measured, and its digestive tract was removed and preserved in 4% formaldehyde. For analysis, the gut contents were examined under appropriate magnification. Items in the gut were identified to species when feasible, and for each taxon we recorded: number, size range, estimated stage of digestion, and estimated percent of the volume represented by that item.

Potential prey

Visual counts enumerated the few potential prey that could be readily seen. Most organisms, however, were too small, or too cryptic, to be assessed this way, and so were sampled with collecting devices. Each assessment of the benthos involved 9 circular corers, 10 cm in diameter, inserted 3 cm into the sand at roughly 5-m intervals along the 50-m tract line, alternating sides from count to count. Each assessment of organisms in the water column involved nets with 0.333-mm mesh that sampled three levels: 1–2 m above the bottom, 1–2 m below the surface, and at the surface. At each level we pushed the net for 5 min at a speed of 30 cm sec^{-1}. The net used in the near-bottom and near-surface collections had a circular opening 1 m in diameter, whereas the net used at the surface had a 20 × 50 cm rectangular opening, half of which was kept above the water while collecting. Illumination during the nocturnal plankton collections was limited to starlight because artificial light might have influenced the zooplankton.

Species of prey and potential prey selected for analysis

A calculated *level of importance* determined which of the taxa identified in samples from either the fish gut contents or the environment would be included in further analysis as prey or potential prey. Although the level-of-importance values are not presented, they are the basis of the list of *organisms present* used in Tables 2–5. This list, which is repeated for each table, includes all taxa from either the fish gut contents, or the environment, that had a level of importance exceeding the arbitrarily selected value 1.0, based on calculations as follows: For taxa in the gut contents (prey), the levels of importance are the *products of their percent frequency of occurrence, and their mean number, or mean volume* (in the case of a few exceptionally large organisms), *in the guts of any one of the fish species studied.* Similarly, for taxa in collections from the environment (potential prey), the levels of importance are the *products of their percent frequency of occurrence and the mean number present in any one collection, calculated for each sampled segment of the habitat*, i.e. the sand, and each of the three levels of the water column. Most of the taxa listed are species, but some higher taxa were included where species could not be distinguished (e.g. natantian larvae), or where such distinction was considered unimportant to this study, and where the level of importance of the group was high (e.g. calanoid copepods). As seen below, only a few of the many organisms collected were excluded from the analysis by this procedure.

Results

During the day the study area appeared as an expanse of open sand, with relatively few visible signs of life (Fig. 2). At night, however, there was a marked increase in both visible numbers and activity among the fishes and other organisms.

Diel patterns in the fishes

Diurnal observations

Of the few species seen during the day (Table 1), some were characteristic of the open-sand habitat, while others were more characteristic of neighboring habitats of rock or algae. Those characteristic of the open sand included three flatfishes: the bothids *Citharichthys stigmaeus* and *Paralichthys californicus*, and the pleuronectid *Pleuronichthys coenosus*. Those more characteristic of rock or algae were the labrids *Halichoeres semicinctus*, and *Semicossyphus pulcher*, the embiotocid *Embiotoca jacksoni*, and the serranid *Paralabrax clathratus*.

The resident flatfishes were inconspicuous due to their concealing coloration and secretive behavior. The two bothids, *C. stigmaeus* and *P. californicus*, frequently went unseen because they were flush with the substrate, often buried, and rarely moved. The small size of *C. stigmaeus* (generally <100 mm SL) helped it go unnoticed (Fig. 3), but *P. californicus* was inconspicuous despite being the largest fish (often >1 m SL) routinely present, day or night (Fig. 4). *P. coenosus*, whose size was intermediate (generally 150–200 mm SL), was the most visible of the three because often its

Fig. 2. The transect line in Ripper's Cove.

Table 1. Fishes counted in the sampled tract at Ripper's Cove.[1,2]

Species	Day n = 3		Night n = 3	
	% freq.	x̄ no.	% freq.	x̄ no.
1. *Heterodontus francisci*, horn shark[3]	–	–	0.33	0.3
2. *Cephaloscyllium ventriosum*, swell shark[2]	–	–	0.33	0.3
3. *Chilara taylori*, cusk-eel	–	–	0.67	2.0
4. *Scorpaena guttata*, sculpin[3]	–	–	1.00	2.0
5. *Paralabrax clathratus*, kelp bass	1.00	3.0[4]	1.00	4.3[5]
6. *Anisotremus davidsoni*, sargo[3]	–	–	0.33	1.0
7. *Umbrina roncador*, croaker	–	–	1.00	2.0
8. *Hyperprosopon argenteum*, walleye perch	–	–	0.67	1.7
9. *Cymatogaster aggregata*, shiner perch	–	–	0.67	3.7
10. *Halichoeres semicinctus*, rock wrasse	1.00	2.3	–	–
11. *Semicossyphus pulcher*, sheephead	0.67	1.0	–	–
12. *Pleuronichthys coenosus*, C-O turbot[6]	–	–	1.00	4.3
13. *Paralichthys californicus*, halibut	–	–	0.33	0.3

[1] The counts generally were consistent with what was seen in the area, but two species unrepresented in the counts frequently were present: *Embiotoca jacksoni*, the black perch, was often present during the day, and *Citharichthys stigmaeus*, the sand dab, was present day and night.

[2] Adults and subadults only. Juvenile embiotocids (surfperches) were numerous and widespread nearshore during this season and some were in the transect at night, including *Embiotoca jacksoni*, *Damalichthys vacca* and *Brachyistius frenatus*.

[3] Not considered in this paper owing to infrequent occurrence in study area.

[4] During the day all those counted in the transects, or seen in the area, were adults.

[5] At night, 77% of those counted in the transects, and about the same proportions of those seen in the area, were subadults.

[6] Frequently present in the transect during the day, although not during the counts.

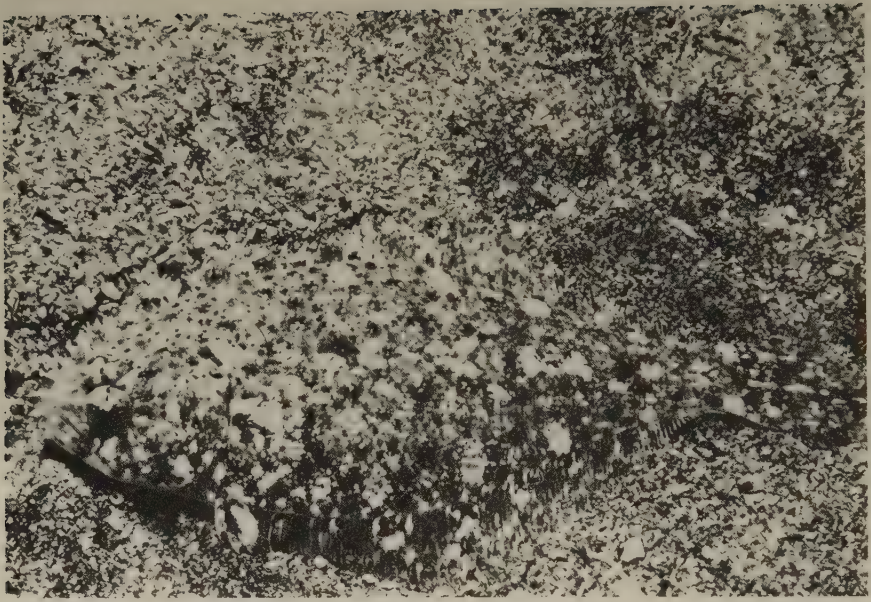


Fig. 3. The speckled sanddab, *Citharichthys stigmaeus*. A laterally compressed body, which permits lying flush on the substrate, and the ability to match its coloration to the color and texture of the surrounding sediment, enables this species to go unseen by both predators and prey. Its relatively large eyes also suit it for activity in dim light.

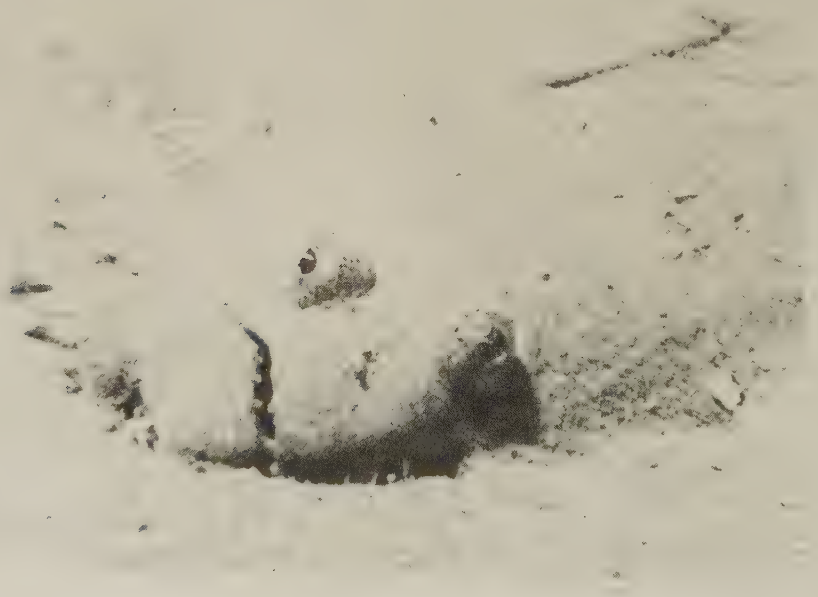


Fig. 4. The California halibut, *Paralichthys californicus*. Its laterally compressed body, large mouth with long canine teeth, and habit of resting motionless under a covering of sand, adapt this species to its habit of ambushing small fishes in the open-sand habitat.

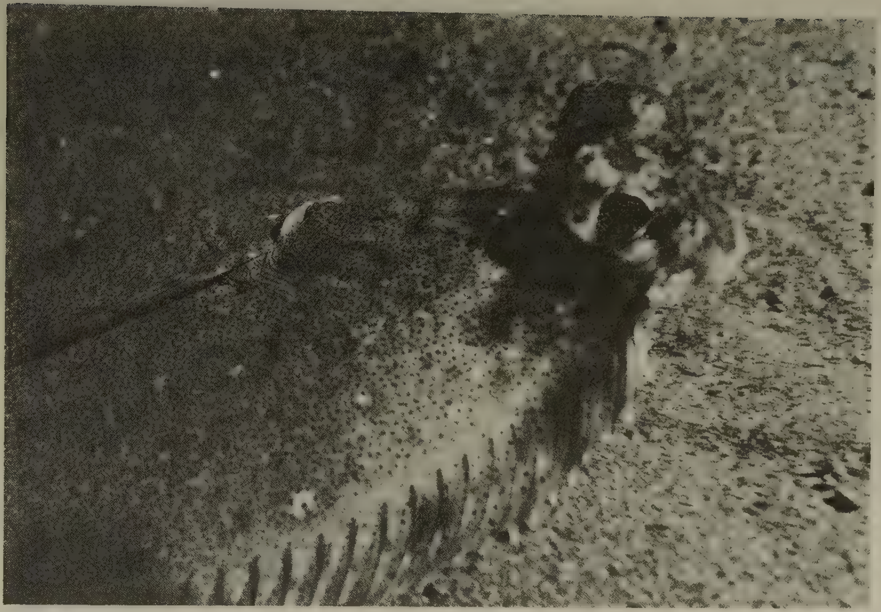


Fig. 5. The C-O sole, *Pleuronichthys coenosus*, with its forebody raised on dorsal and anal fins, and its exceptionally large, highly mobile eyes set on either side of a high, narrow ridge. This fish is suited to scan the surrounding sea floor in dim light, and its downward-projecting mouth is suited to be driven into the sediment for prey.

forebody was elevated on dorsal and anal fins, so that its head was poised above the substrate. From this position, *P. coenosus* scanned its surroundings with mobile eyes oriented vertically on either side of a high, narrow ridge, almost as if in a turret (Fig. 5). Although *P. coenosus* generally appeared inactive in daylight, occasionally an individual that had been immobile moved a meter or more across the bottom, then drove its head into the sand, apparently to feed.

Individuals of the four species more characteristic of neighboring habitats were relatively conspicuous when they swam into the study area. *Halichoeres semicinctus, Semicossyphus pulcher* and *Embiotoca jacksoni* continually moved about and foraged in the sand, whereas *Paralabrax clathratus* often hovered close above the sand (Fig. 6). Usually *H. semicinctus* was solitary, and much of the time made close visual inspections of the substrate (Fig. 7). Frequently it picked at the surface of the sand, apparently targeting individual prey, but also incidentally ingesting some sediment. *S. pulcher,* too, usually was solitary, but spent far less time than *H. semicinctus* overtly inspecting the substrate and made fewer attempts to feed. It appeared to target individual prey, but often rooted in the sand (Fig. 8), and in so doing ingested much sediment, most of which it vented from its mouth and gill openings. *E. jacksoni*, which usually foraged in small groups of two or more, did not spend the time in close visual inspection so characteristic of *H. semicinctus* but spent more time ingesting food. Typically it took mouthfuls of sediment, and only then appeared to distinguish edible from inedible materials before venting clouds of debris from mouth and gill openings. Thus, it did not appear to target individual prey, as did the others and, also unlike the others, it appeared to take sediment intentionally (see Schmitt & Coyer 1982, Laur & Ebeling 1983). We only occasionally saw *P. clathratus* feed during the day; its attacks, all launched from its hovering position at prey on or close to the sand, were infrequent.

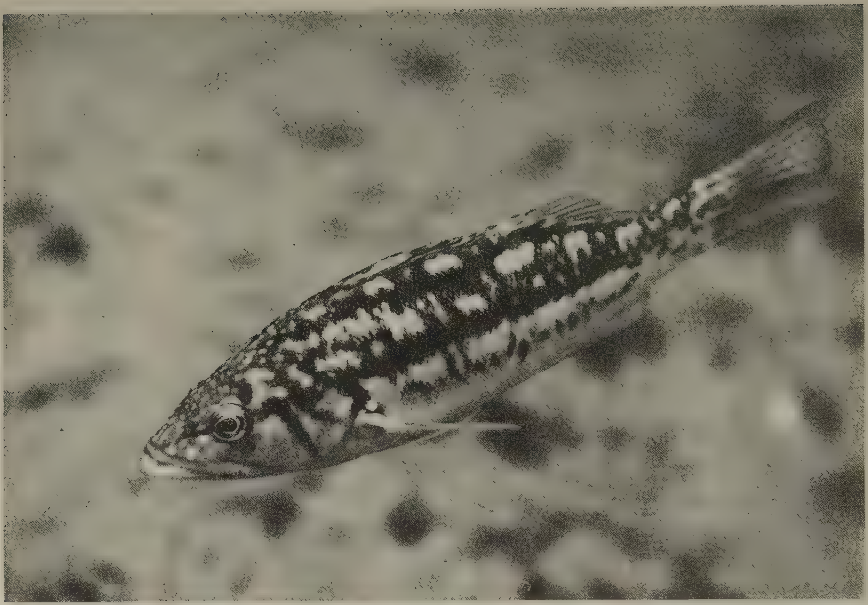


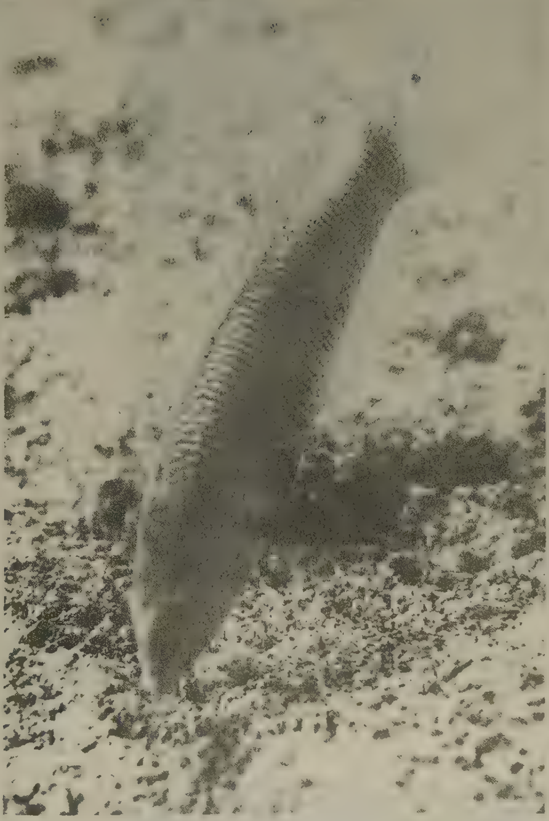
Fig. 6. The kelp bass, *Paralabrax clathratus*. The coloration of this species is better-suited to the kelp forest which is its regular habitat. Nevertheless, its stalking mode of predation is suited to detect and capture prey that are only occasionally exposed or otherwise vulnerable – which is characteristic of many small organisms in the open-sand habitat.

Nocturnal observations

Of the increased number of fishes seen in the study area after dark (Table 1), some were in the open-sand habitat during both day and night, whereas others were there only at night. Of the species typically in the open-sand habitat during both day and night, three were described above – the flatfishes *Citharichthys stigmaeus*, *Paralichthys californicus*, and *Pleuronichthys coenosus*. The fourth, the ophidiid *Chilara taylori*, was not seen in daylight because it was buried in the sand. *C. taylori* did not emerge from the sand until about 3 h after sunset, which was at least 2 h after the other nocturnal feeders had become active. When feeding, *C. taylori* swam close to the bottom, and probed in the sand with its barbel-like pelvic fins (Fig. 9). It reentered the sand about 3 h before sunrise, which was at least 2 h before the other nocturnal feeders in the study area ceased foraging. Owing to its distinctive diel activity pattern, *C. taylori* was sampled for gut contents between midnight and 0100 h.

The fishes that entered the study area only at night used the open-sand habitat as a major feeding ground. These included the embiotocids *Hyperprosopon argenteum* (Fig. 10) and *Cymatogaster aggregata* (Fig. 11), and also the sciaenid *Umbrina roncador* (Fig. 12). Foraging individuals of *H. argenteum* swam loosely spaced in groups in the water column, whereas those of *C. aggregata* hovered loosely spaced in groups, or as individuals, within a meter of the sand. Although prominent over the open sand at night, these three species spent the day in relatively inactive schools in neighboring habitats shoreward: *H. argenteum* and *C. aggregata* schooled over rocks and algae, while *U. roncador* schooled over sand near the beach. (Many *C. aggregata* also foraged by day in small groups on the sand close to rocks, and some *U. roncador* also foraged by day near their diurnal schools.)

The daytime foragers noted above as more characteristic of neighboring habitats – *Halichoeres semicinctus*, *Semicossyphus pulcher*, *Embiotoca jacksoni*, and *Paralabrax clathratus* – had returned



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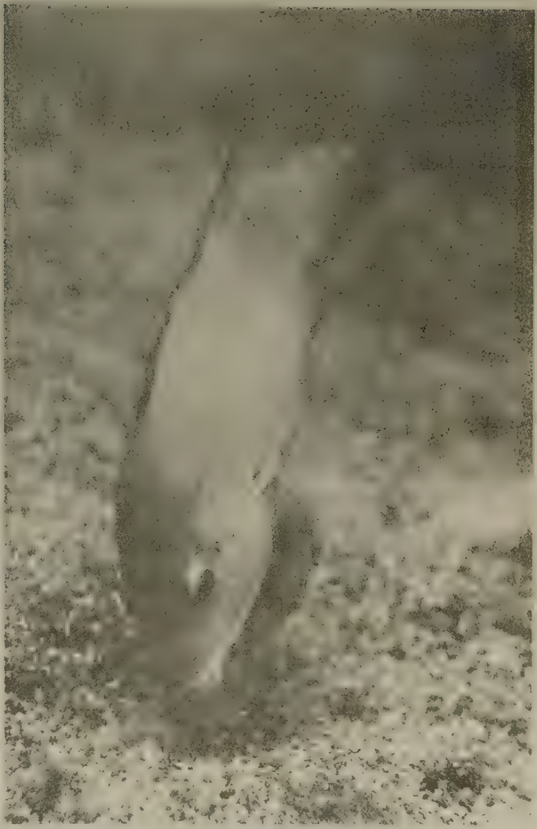

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Fig. 7. The rock wrasse, *Halichoeres semicinctus*. The strictly diurnal habits and manner of intently gazing at the substrate for long periods before plucking, suggest that this species depends on acute vision to detect cryptic prey. Its pointed snout and small mouth with large canine teeth at the front of its jaws are well-adapted to pluck small organisms from the sand.

Fig. 8. The California sheephead, *Semicossyphus pulcher*. The large mouth, strong canine and pharyngeal teeth, with highly developed ability to winnow edibles from other material, permit this species to excavate, crush and ingest the heavily armored, often buried organisms, like mollusks, that are major prey. Note cloud of debris being ejected from gill openings.

to their more typical habitats by nightfall, where, like others of their kind, they sheltered amid rocks and algae (Fig. 13). The increased numbers of *P. clathratus* in the study area at night (Table 1) involved primarily subadults that were not there during the day. (Most *P. clathratus* in the study area by day were adults.) The subadult *P. clathratus* in Ripper's Cove generally were in the rock and algae habitats during daylight, but at nightfall many of them scattered over the open sand. (See Hobson et al. 1981)

Diel patterns in potential prey

Other than fishes, the only species readily observed in the study area was the holothurian *Parastichopus parvimensis*, nine of which were counted within the sampling tract during one daytime transit. With closer visual inspection of ten 0.25-m^2 quadrats set at 5-m intervals along the tract line, three additional species were enumerated. These were (values given are frequency of occurrence: mean number: range of numbers) the tubiculous polychaete *Spiochaetopterus costarum* (1.00:58.2:18–102), the

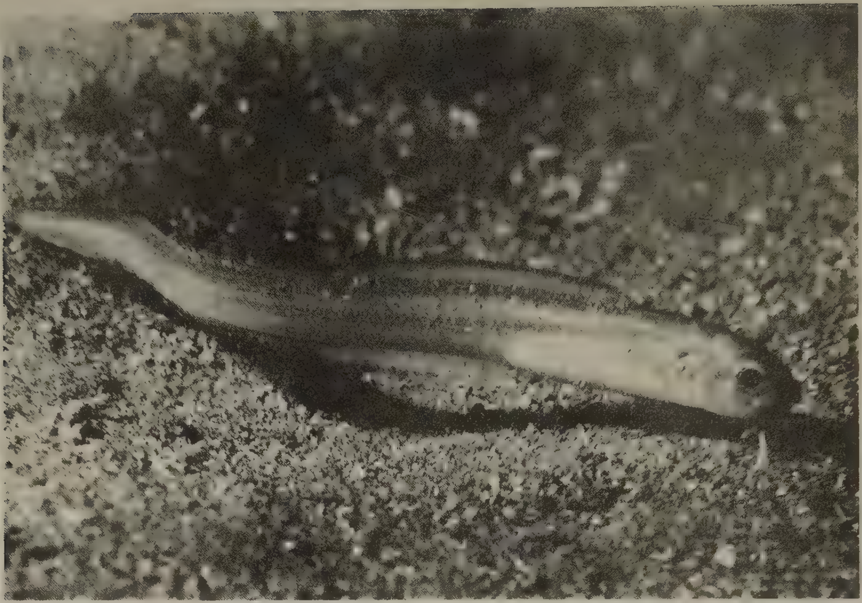

Fig. 9. The spotted cusk-eel, *Chilara taylori.* The eel-like body of this fish permits it to shelter in the sand by day. Although its large eyes enhance its ability to see prey and predators during its nocturnal forays, apparently at least much of its prey are detected by its modified pelvic fins, shown here probing the sand.

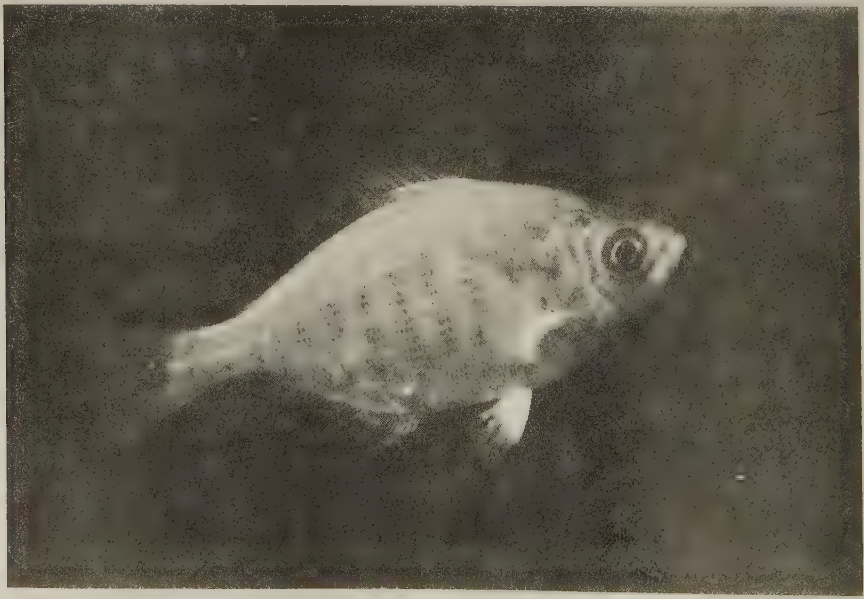

Fig. 10. The walleye surfperch, *Hyperprosopon argenteum.* Exceptionally large eyes suit this planktivore for its nocturnal hunting habits. Its upturned mouth, a characteristic of specialized planktivores, results from a shortened snout that places its eyes in position for binocular vision when targeting on small prey close ahead (W. A. Starck, cited in Rosenblatt 1967)

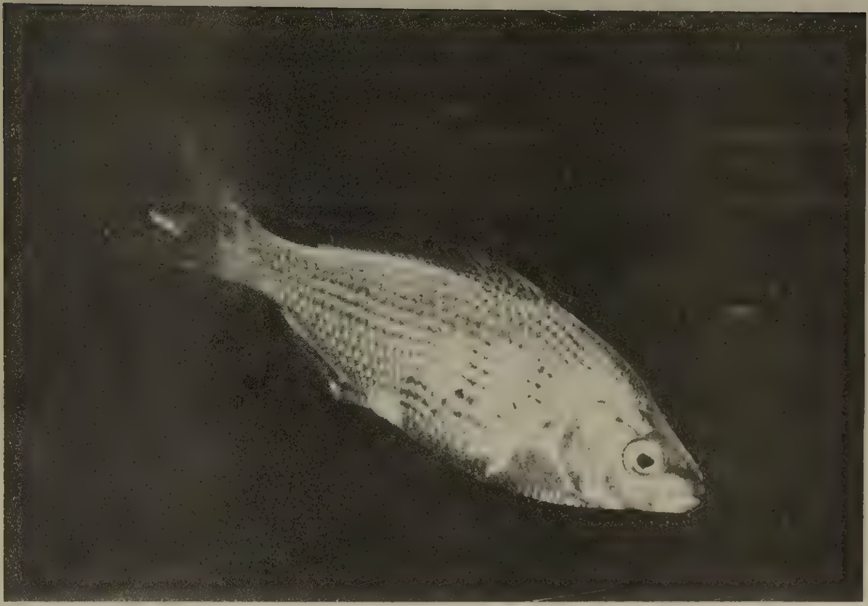

Fig. 11. The shiner perch, *Cymatogaster aggregata.* With generalized trophic features, this species is more versatile in its feeding than the others (see Hobson et al. 1981). Its slightly underslung lower jaw, however, is well-suited to its major adult feeding mode of taking prey on or close to the sand. It does this primarily at night, when reflected moonlight or starlight probably permits visual nocturnal hunting even with eyes not noticeably large.

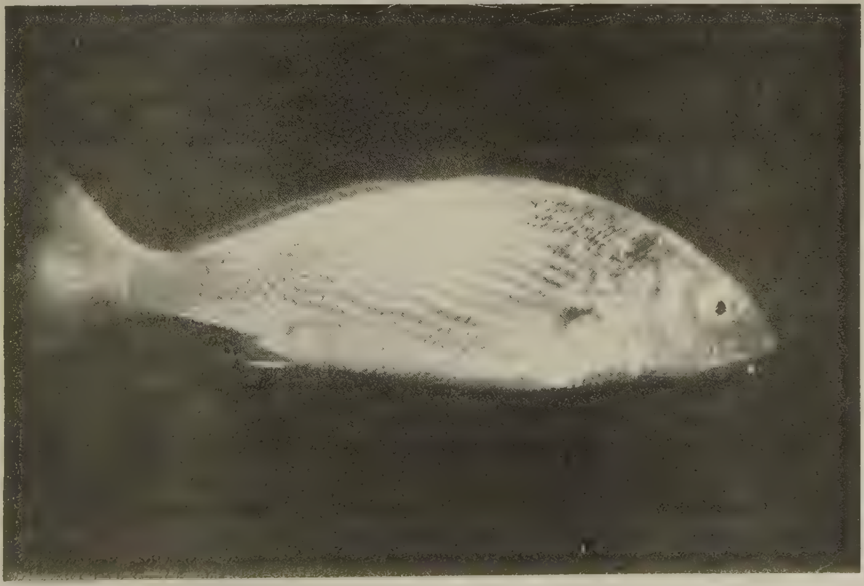

Fig. 12. The yellowfin croaker, *Umbrina roncador.* The stout conical snout projecting above the mouth, and underslung lower jaw with a single, short barbel, suit this fish for foraging in the sand.

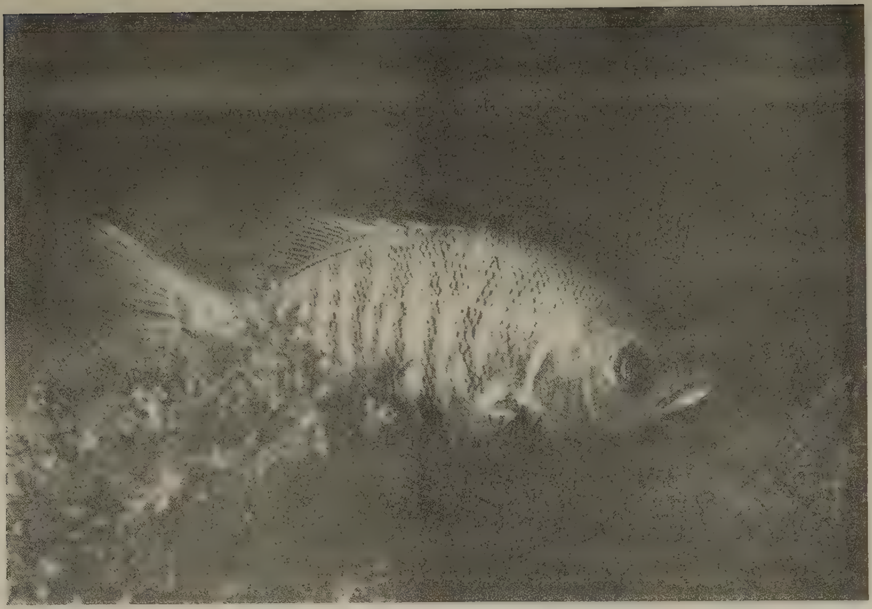

Fig. 13. The black perch, *Embiotoca jacksoni*, a diurnal feeder, here in benthic algae at night. Although the coloration of this species is better-suited to habitats rich in vegetation, it nevertheless finds the open-sand habitat a productive foraging ground because its ability to winnow edibles from inedibles allows it to extract the many prey in heavy loads of ingested sediment.

phoronid *Phoronis vancouverensis* (0.2:0.2:0–1), and the gastropod *Olivella biplicata* (0.2:0.2:0–1). Perhaps the most visible biotic features (certainly the most visible in Fig. 1) were the sand castings produced by *P. parvimensis* (occurrence in quadrats was 0.9:1.9:0–4). These forms were counted just once, because experience elsewhere (unpublished data) had indicated that during this study their numbers would not change in ways relevant to topics considered here.

The vast majority of organisms considered as potential prey could not be assessed visually, but our collections showed that many were distributed differently between day and night (Table 2). Particularly striking, great numbers of them, mostly crustaceans, migrated upward in the water column after dark, including many that were benthonic by day. Thus, the numbers of zooplankters collected after dark in the upper level of the water column and at the surface increased almost fourfold over the numbers that were collected there during the day. Although the vertical migrations of most were limited, at least four species – the ostracods *Parasterope* sp. and *Rutiderma lomae* (males only), the isopod *Eurydice caudata*, and the gammaridean *Paraphoxus heterocuspidatus* – migrated from the benthos all the way through the water column to concentrate at the water's surface. Although most diel vertical migrations involved movement upward at night, limited evidence indicates the reverse in at least some fish larvae (Table 2).

Trophic relationships

Each of the fish species that foraged in Ripper's Cove took just certain of the many organisms present – some by day (Table 3), others at night (Table 4). As a group, however, they consumed virtually all sizes of every species identified in our samples of potential prey in the environment (Tables 2 and 5) – except the holoplankton, none of which were taken. With two exceptions (noted below), these fishes were benthivores, and those that foraged by day took many prey of species also taken by those that foraged at night. Of the 31 prey categories distinguished as species, 21 (67.7%) were taken

Table 2. Diel distributions of organisms in Ripper's Cove.[1]

Organisms present[2]	Day				Night			
	Bottom (3 cm × 1 m^2)	Water column (10 m × 1 m^2)			Bottom (3 cm × 1 m^2)	Water column (10 m × 1 m^2)		
	In sand n = 27	Lower 5 m n = 3	Upper 5 m n = 3	Surface 0.1 m n = 3	In sand n = 27	Lower 5 m n = 3	Upper 5 m n = 3	Surface 0.1 m n = 3
FORAMINIFERA								
Tretomphalus sp.	0	0.55	0	0	0	0	2.35	0.65
POLYCHAETA								
Nothria stigmatis	367.97	0	0	0	296.66	0	0	0
Owenia collaris	278.84	0	0	0	282.66	0	0	0
Spiochaetopterus costarum	38.20	0	0	0	38.20	0	0	0
Others	1.097.53	0	0	0	957.48	0	0	0
MOLLUSCA								
Veligers	0	0.40	0.05	0	0	0.40	2.10	0.69
Crenella divaricata	52.20	0	0	0	42.02	0	0	0
Parvilucina approximata	80.21	0	0	0	108.23	0	0	0
Lyonsia californica	14.01	0	0	0	24.19	0	0	0
Tellina modesta	357.78	0	0	0	376.88	0	0	0
CLADOCERA								
Evadne sp.	0	55.15	48.75	0.04	0	48.80	123.60	7.65
OSTRACODA								
Euphilomedes carcharodonta	471.10	0	0	0	631.53	0	0	0.30
Parasterope sp.	188.44	0	0	0	122.23	1.45	0.25	4.35
Rutiderma lomae	19.10	0	0	0	14.01	0	0.09	1.09
Others	127.32	0	0	0	147.70	1.05	0.20	0
COPEPODA								
Calanoids, various spp.	0	619.85	47.85	1.95	95.5	613.05	726.20	19.65
Cyclopoids, various spp.	14.01	2.15	0.60	0	0	4.00	6.60	0.80
Harpacticoids, various spp.	14.01	0.30	0	0	71.30	0	0	0.02
MYSIDACEA								
Erythropinid sp.	0	0	0	0	14.01	15.65	0.85	0
Siriella pacifica[3]	0	0	0	0	0	4.35	0.70	2.87
Others	5.09	0	0	0	5.09	0.35	0.05	0.04
CUMACEA								
Cyclaspis nubila	1,508.79	0	0	0	1,320.35	8.85	0.35	0
Others	42.02	0	0	0	61.12	0.35	0.05	0.85
TANAIDACEA								
Leptochelia dubia	292.85	0	0	0	240.64	0.10	1.00	0.05
Others	8.91	0	0	0	0	0	0	0
ISOPODA								
Eurydice caudata	5.09	0	0	0	5.09	0.25	0.15	3.01
Exosphaeroma rhomburum	47.11	0	0	0	28.01	0.05	0	0
Others	0	0	0	0	0	0	0.10	0
GAMMARIDAE								
Acuminodeutopus heteruropus	11.002.06	0	0	0	12,456.73	0	0	0
Ampelisca cristata	816.15	0	0	0	1,187.93	0.15	0	0
Amphideutopus oculatus	420.17	0	0	0	495.29	0	0	0
Batea transversa[3]	0	0	0	0	28.01	11.85	2.05	0.01
Ericthonias braziliensis	891.27	0	0	0	1,051.70	0	0	0
Metaphoxus frequens	1.381.46	0	0	0	1.838.25	0.05	0	0.01
Monoculodes hartmanae	240.64	0	0	0	263.56	2.05	0	0
Paraphoxus heterocuspidatus	2,810.04	0	0	0	2,438.25	0.05	0	0.50

Table 2. (Continued).

Organisms present[2]	Day				Night			
	Bottom (3 cm × 1 m^2)	Water column (10 m × 1 m^2)			Bottom (3 cm × 1 m^2)	Water column (10 m × 1 m^2)		
	In sand n = 27	Lower 5 m n = 3	Upper 5 m n = 3	Surface 0.1 m n = 3	In sand n = 27	Lower 5 m n = 3	Upper 5 m n = 3	Surface 0.1 m n = 3
Photis brevipes	85.31	0	0	0	113.32	0	0	0
Rudilemboides stenopropodus	406.16	0	0	0	296.66	0	0	0
Synchelidium rectipalmum	240.64	0	0	0	226.64	0.65	0	0
Others	654.45	0	0	0	1,137.00	0.75	0.90	0
CAPRELLIDAE								
Caprella pilidigita	5.09	0	0	0	14.01	0	0	0
Mayerella banksia	296.66	0	0	0	179.53	0	0	0
Others	85.31	0	0	0	28.01	0.40	0	0.01
NATANTIA								
Larvae and juveniles	0	0	0.05	0.02	10.19	63.95	91.20	0.08
Crangon holmsi	5.09	0	0	0	8.91	0	0	0
Others	0	0	0	0	0	0	0	0
REPTANTIA								
Zoeae	0	0	0	0	5.09	11.10	27.60	0.50
Others	0	0	0	0	0	0	0.10	0
ECHINODERMATA								
Dendraster excentricus	56.02	0	0	0	61.12	0	0	0
Others	28.01	0	0	0	43.29	0	0	0
CHAETOGNATHA								
Various spp.	0	2.85	4.15	0.05	0	2.25	14.55	0.16
LARVACEA								
Various spp.	0	2.70	0	0	0	1.15	9.15	0.90
FISHES								
Eggs (planktonic)	0	42.15	184.65	2.27	0	20.50	37.45	4.33
Larvae	0	0.25	0.10	0.01	0	1.10	0.25	0
Others	0	0	0	0	8.91	0	0	0.01
MISCELLANEOUS[4]	117.14	2.50	4.50	0.06	81.49	0.01	0.13	0.09

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[1] Tabulated values are estimated mean numbers present within the designated segments of a hypothetical 1-m^2 × 10-m high column that extends from the sand to the water's surface. The values were derived as follows: (1) *Bottom, in sand.* – The estimated mean numbers of organisms in the sand (to a depth of 3 cm) at the base of the column were extrapolated from the mean numbers collected in the circular cores ($r = 0.05$ m) by multiplying by 127.324 (based on the relationships of $A = \pi r^2$). (2) *Water column, lower.* – The estimated mean numbers in the lower 5 m of the water column were extrapolated from the mean number collected in the circular plankton net ($r = 0.5$ m) 2–3 m above the sand by multiplying by 0.0787 (based on the volume of water filtered during each collection, 70.868 m^3, as calculated from collection time and net speed: see Methods). (3) *Water column, upper.* – The estimated numbers in the upper 5 m of the water column were extrapolated as for the lower water column, but from the collections within 2–3 m of the water's surface. (4) *Water column, surface.* – The estimated mean numbers in the column within 0.1 m of the surface were extrapolated from mean numbers collected in the modified plankton net (0.5 m × 0.2 m rectangular opening, half-submerged: see Methods) by multiplying by 0.0222 (based on the water filtered, 4.5 m^3, as calculated from collection time and net speed).

[2] The list includes all taxa designated as important, either in the habitat or in the gut contents, by the procedures described in Methods. The category 'others' in the list includes the species whose calculated level of importance was below the designated level, and also a variety of individuals that could not be identified to species (presumably many of these were young stages of species distinguishable only as adults and these are included among the unidentified taxa of that group).

[3] *Siriella pacifica* and *Batea transversa* inhabit algae during the day (Hobson & Chess 1976). Their absence in our daytime collections suggests that those we collected at night came from daytime shelter in neighboring habitats.

[4] Includes those collected in small numbers that are not referable to one of the other categories. Figures for diurnal water column inflated by large numbers of bryozoan and cirripedian larvae that were present one day.

Table 3. Mean numbers of prey taken by the major fish species during the day from among the organisms present in Ripper's Cove.

Fish species[1]
1. *Paralabrax clathratus* n = 4 (1 empty) 115.9 (89–140) mm SL
2. *Embiotoca jacksoni* n = 4 (0 empty) 137.8 (113–165) mm SL
3. *Halichoeres semicinctus* n = 10 (0 empty) 171.1 (106–218) mm SL
4. *Semicossyphus pulcher* n = 6 (0 empty) 221.7 (206–265) mm SL
5. *Citharichthys stigmaeus* n = 4 (0 empty) 81.3 (63–94) mm SL
6. *Pleuronichthys coenosus* n = 4 (2 empty) 180 (170–190) mm SL

Organisms present[2]	1	2	3	4	5	6
FORAMINIFERA						
Tretomphalus sp.	0	0	0	0	0	0
POLYCHAETA						
Nothria stigmatis	0	0	0	0	0	0.5
Owenia collaris	0	0	1.0	0.3	0	0
Spiochaetopterus costarum	0	3.8[3]	7.7	0.3	1.0	0
Others	0	0	4.1	4.0	1.0	1.0
MOLLUSCA						
Veligers	0	0	0	0	0	0
Crenella divaricata	0	3.8	0.3	3.3	0	0
Parvilucina approximata	0	0	0.1	3.2	0	0
Lyonsia californica	0	0.3	0.3	1.8	0	0
Tellina modesta	0	0	0.4	9.7	0	0.5
Others	0	0.3	1.4	8.6[4]	0	0
CLADOCERA						
Evadne sp.	0	0	0	0	0	0
OSTRACODA						
Euphilomedes carcharodonta	0.3	2.3	0.8	1.2	0	0
Parasterope sp.	0	7.0	0.8	0.3	0	0
Rutiderma lomae	0	0	0	0	0	0
Others	0.3	1.5	0.3	0	0	0
COPEPODA						
Calanoids, various spp.	0	0	0	0	0	0
Cyclopoids, various spp.	0	0	0	0	0	0
Harpacticoids, various spp.	0	0	0	0	0	0
MYSIDACEA						
Erythropinid sp.	0	0	0	0	0	0
Siriella pacifica	0	0	0	0	0	0
Others	0	0	0	0	0	0
CUMACEA						
Cyclaspis nubila	0.3	13.8	3.5	0	0.3	0
Others	0	0.5	0	0	1.0	0
TANAIDACEA						
Leptochelia dubia	0.3	6.5	3.6	0	0	0
Others	0	0	0	0	0	0
ISOPODA						
Eurydice caudata	0	0	0	0	0	0
Exosphaeroma rhomburum	0	0	0	0	0	0
Others	0	4.3	0	0	0.8	0
GAMMARIDEA						
Acuminodeutopus heteruropus	10.7	126.3	22.9	0.3	4.3	0
Ampelisca cristata	0.7	3.3	0.7	11.2	1.5	24.5
Amphideutopus oculatus	0	2.1	0.1	0	0	0
Batea transversa	0	0	0	0	0	0
Ericthonias braziliensis	1.0	16.3	1.5	0	0.5	0
Metaphoxus frequens	0.7	5.5	1.6	0	0	0.5
Monoculodes hartmanae	0	1.5	0.8	0.3	1.0	0

Table 3. (Continued).

Organisms present[2]	Fish species 1	2	3	4	5	6
Paraphoxus heterocuspidatus	0	0.8	0.6	1.5	0	0
Photis brevipes	0	13.8	45.2	0.5	0	0
Rudilemboides stenopropodus	0.7	3.3	0.9	1.0	0	0
Synchelidium rectipalmum	0	0.8	0.1	0	0	0
Others	5.0	87.7	28.3	15.2	0.8	0
CAPRELLIDAE						
Caprella pilidigita	0.3	0	4.0	0	0	0
Mayerella banksia	1.0	1.0	3.8	0	0.3	0
Others	4.3	2.0	0	0	0	0
NATANTIA						
Larvae and juveniles	0	0	0	0	0	0
Crangon holmsi	0	0	0	0	0	0
Others	0	0	0.1	0.5	0	0
REPTANTIA						
Zoeae	0	0	0	0	0	0
Others	0	0	0	0.5	0	0
ECHINODERMATA						
Dendraster excentricus	0	0	0.3	9.3	0	0
Others	0	0		0.3	0	0
CHAETOGNATHA						
Various spp.	0	0	0	0	0	0
LARVACEA						
Various spp.	0	0	0	0	0	0
FISHES						
Eggs (pelagic)	0	0	0	0	0	0
Larvae	0	0	0	0	0	0
Others	1.3	0	0	0	0	0
MISCELLANEOUS	0	0	1.3	4.0	0	0
SAND (x̄ % of diet volume)	6.3	17.3	10.6	8.5	0	7.5

[1] For all species, size range of specimens approximated size range of individuals present.

[2] See Footnote 1, Table 2.

[3] Tube fragments only.

[4] Fragments of relatively large, heavily-shelled bivalves (including *Americardium biangulata*) and gastropods (*Lirularia* sp. and *Olivella baetica*). Most larger items in the gut contents of *S. pulcher* even when fresh, were crushed. Often this made identification difficult, and measurements only estimates.

during both day and night, whereas only 4 (12.9%) were taken strictly by day, and 6 (19.4%) were taken just at night. Species not taken in similar numbers during both day and night included the more sedentary, heavily armored forms like mollusks and echinoids, which were prey primarily of the diurnal feeders, and the polychaetes, which were prey primarily of the nocturnal feeders. The two fish species that did not forage on the benthos were *Paralichthys californicus* and *Hyperprosopon argenteum*. We did not examine gut contents of *P. californicus* from Ripper's Cove, but reportedly the species feeds primarily by day (Haaker 1975) on smaller fishes of the types considered here as predators (Limbaugh 1955, Quast 1968). *H. argenteum*, a nocturnal planktivore, did not prey on holoplankters (most <2 mm; Table 5), even though holoplankters constituted the majority of nighttime zooplankton; rather, it preyed entirely on certain forms (most >2 mm; Table 5) that were among the zooplankton only after dark (Table 2).

Table 4. Mean numbers of prey taken by the major fish species at night from among the organisms present in Ripper's Cove.

Fish species[1]
1. *Chilara taylori* n = 11 (1 empty) 129.9 (109–152) mm SL
2. *Paralabrax clathratus* n = 11 (5 empty) 100.1 (72–148) mm SL
3. *Umbrina roncador* n = 8 (0 empty) 201 (191–228) mm SL
4. *Cymatogaster aggregata* n = 15 (1 empty) 98.6 (70–109) mm SL
5. *Hyperprosopon argenteum* n = 10 (0 empty) 110.5 (110–148) mm SL
6. *Citharichthys stigmaeus* n = 8 (2 empty) 56 (42–65) mm SL
7. *Pleuronichthys coenusus* (sm) n = 5 (0 empty) 86 (60–115) mm SL
8. *Pleuronichthys coenosus* (lg) n = 5 (1 empty) 153.3 (140–167) mm SL

Organisms present[2]	1	2	3	4	5	6	7	8
FORAMINIFERA								
Tretomphalus sp.	0	0	0	0	0	0	0	0
POLYCHAETA								
Nothria stigmatis	0	0	24.9	0	0	0.2	0.6	2.3
Owenia collaris	0	0	0	0	0	0	0	0
Spiochaetopterus costarum	0	0	0	2.1	0	6.0	0	76.5
Others	0	0	2.3	0	0.3	0	0.2	2.3
MOLLUSCA								
Veligers	0	0	0	0	0	0	0	0
Crenella divaricata	0	0	0	0.1	0	0	0	0
Parvilucina approximata	0	0	0	0	0	0	0	0
Lyonsia californica	0	0	0.1	0.1	0	0	0	0
Tellina modesta	0	0	0	0	0	0	0	0
Others	0	0	0.1	0	0	0	0	0.3
CLADOCERA								
Evadne sp.	0	0	0	0	0	0	0	0
OSTRACODA								
Euphilomedes carcharodonta	0	0	0	1.8	0.2	0	0	0
Parasterope sp.	0	0	0.3	0.1	2.3	0	0	0
Rutiderma lomae	0	0	0	0	0.3	0	0	0
Others	0	0	0	0.4	0.1	0	0	0
COPEPODA								
Calanoids, various spp.	0	0	0	0	0	0	0	0
Cyclopoids, various spp.	0	0	0	0	0	0	0	0
Harpacticoids, various spp.	0	0	0	0	0	0	0	0
Others	0	0.2	0	0	0	0	0	0
MYSIDACEA								
Erythropinid sp.	0	0.2	0	0	0	0	0	0
Siriella pacifica	0	0	0	0	1.6	0	0	0
Others	0	0.7	0	0	0.2	0	0	0
CUMACEA								
Cyclaspis nubila	0.2	0.2	0.4	9.3	10.9	0.3	0.4	0
Others	0	0	0.3	0.1	2.6	0	0	0
TANAIDACEA								
Leptochelia dubia	0	0	0.3	5.1	3.0	0	0	0
Others	0	0	0	0	0.4	0	0	0
ISOPODA								
Eurydice caudata	0	0	0	0	0.2	0	0	0
Exosphaeroma rhomburum	0	0.2	0	0.4	0.1	0	0	0
Others	0	0.2	0	0.1	1.0	0	0	0
GAMMARIDEA								
Acuminodeutopus heteruropus	1.5	0.2	1.5	66.9	0	1.5	2.2	0

Table 4. (Continued).

Organisms present[2]	Fish species 1	2	3	4	5	6	7	8
Ampelisca cristata	7.2	0.5	35.3	3.8	4.4	2.0	8.4	4.8
Amphideutopus oculatus	0.6	0.3	1.5	1.0	0	0	0.4	0
Batea transversa	0	0.3	0	0.1	85.3	0	0	0
Ericthonias braziliensis	0.2	0	0	3.5	0	0	0	0
Metaphoxus frequens	0	0	0.4	1.1	1.0	0	0	0.3
Monoculodes hartmanae	0.4	0	0.6	1.7	1.3	0.2	0	0.3
Paraphoxus heterocuspidatus	0.1	0	3.4	0.1	2.4	0.2	0	0
Photis brevipes	1.9	0	2.3	4.1	0	2.4	2.4	4.0
Rudilemboides stenopropodus	0	0.2	0.5	4.6	0	0.2	1.2	0
Synchelidium rectipalmum	0	0	0.3	0.4	0.1	0	0	0
Others	0.8	0.3	1.4	25.6	37.3	0.5	0.4	1.5
CAPRELLIDAE								
Caprella pilidigita	0	0.3	0	0.9	9.7	0	0	0.3
Mayerella banksia	0	0	0	0.2	0	0	0	0.8
Others	0	1.6	0.3	0.4	0	0	0	0
NATANTIA								
Larvae and juveniles	0	0	0	0	0	0	0	0
Crangon holmsi	0.8	0	0.4	0	0	0	0	0
Others	0	0.2	0.1	0	0.1	0.2	0.2	0
REPTANTIA								
Zoeae	0	0	0	0	0	0	0	0
Others	0	0	0	0	0	0	0	0
ECHINODERMATA								
Dendraster excentricus	0	0	0	0	0	0	0	0
Others	0	0	0	0	0	0	0	0
CHAETOGNATHA								
Various spp.	0	0	0	0	0	0	0	0
LARVACEA								
Various spp.	0	0	0	0	0	0	0	0
FISHES								
Eggs (pelagic)	0	0	0	0	0	0	0	0
Larvae	0	0	0	0	0	0	0	0
Others	0.1	0.3	0	0	0	0	0	0
MISCELLANEOUS	0	0	0.4	0	0.9	0	0.4	0
SAND ($\bar{x}$ % of diet volume)	0	0	5.5	14.9	0	0	0	0

[1] See Footnote 1, Table 3.

[2] See Footnote 1, Table 2.

Discussion

Structurally and behaviorally, the fishes that frequented the open-sand habitat in Ripper's Cove were a diverse group, and much of their diversity related to the ways they extracted food from the environment. Their thoroughness in exploiting the prey resources of this habitat resulted from having an array of feeding adaptations that closely matched the array of feeding opportunities present. Based on these facts, and considering diurnal and nocturnal conditions separately, we first discuss how characteristic trophic features in these species meet requirements of foraging in the open-sand habitat. We then generalize from these findings to consider predator-prey relations as primary

Table 5. Sizes of organisms in collections from the habitat and in gut contents of the fishes.

Organisms present[1]	Size ranges (mm)					
	Day			Night		
	Sand	Plankton	Prey	Sand	Plankton	Prey
FORAMINIFERA						
Tretomphalus sp.	–	0.3–0.5	–	–	0.3–0.7	–
POLYCHAETA						
Nothria stigmatis	5.0–20.0	–	10.0	4.0–30.0	–	8.0–28.0
Owenia collaris	10.0–26.0	–	N.R.[2]	12.0–35.0	–	N.R.
Spiochaetopterus costarum	12.0	–	10.0–15.0	10.0–20.0	–	2.0–15.0
Others	2.0–30.0	–	8.0–12.0	1.0–55.0	3.0–18.0	8.0–15.0
MOLLUSCA						
Veligers	–	0.5	–	–	0.5–1.0	–
Crenella divaricata	2.0–3.0	–	1.0–4.0	1.0–3.0	–	2.0–4.0
Parvilucina approximata	2.0–5.0	–	3.0–5.0	2.0–5.0	–	–
Lyonsia californica	2.0–15.0	–	4.0–16.0	4.0–10.0	–	4.0
Tellina modesta	1.0–10.0	–	3.0–7.0	1.0–7.0	–	–
Others	1.0–22.0	–	3.0–10.0	1.0–20.0	–	3.0
CLADOCERA						
Evadne sp.	–	0.5–2.0	–	–	0.5–1.0	–
OSTRACODA						
Euphilomedes carcharodonta	0.5–2.5	–	1.0–2.0	1.0–3.0	2.0–3.0	1.0–2.0
Parasterope sp.	1.0–2.0	1.0	1.0–2.0	1.0–2.0	1.0–2.5	1.0–2.0
Rutiderma lomae	1.5–2.0	–	–	1.0–2.0	1.5	2.0
Others	0.4–3.0	–	1.0–2.0	0.8–2.0	1.0–2.0	2.0
COPEPODA						
Calanoids, various spp.	–	1.0–2.0	–	–	1.0–2.0	–
Cyclopoids, various spp.	–	1.0	–	–	1.0	–
Harpacticoids, various spp.	0.8–1.0	0.5–1.0	–	0.5–0.8	0.8–1.0	–
Others	0.4	–	–	–	–	2.0
MYSIDACEA						
Erythropinid sp.	–	–	–	4.0	2.0–5.0	3.0
Siriella pacifica	–	–	–	–	3.0–12.0	5.0–8.0
Others	4.0	–	–	4.0	3.0–8.0	5.0–10.0
CUMACEA						
Cyclaspis nubila	2.0–6.0	–	2.0–5.0	2.0–6.0	2.0–5.0	3.0–4.0
Others	1.0–3.0	0.5	2.0	2.0–4.0	1.0–2.0	2.0–5.0
TANAIDACEA						
Leptochelia dubia	1.0–5.0	–	2.0–5.0	1.0–5.0	1.0–3.0	2.0–4.0
Others	3.0	–	–	–	–	–
ISOPODA						
Eurydice caudata	2.0	–	–	2.0	2.0–5.0	2.0–6.0
Exosphaeroma rhomburum	1.0–3.0	–	–	2.0–3.0	2.0–4.0	2.0–3.0
Others	–	–	–	–	1.0–2.0	2.0
GAMMARIDEA						
Acuminodeutopus heteruropus	1.0–4.0	–	1.0–3.0	1.0–3.0	–	1.0–2.0
Ampelisca cristata	2.0–11.0	–	3.0–11.0	2.0–13.0	4.0–6.0	3.0–9.0
Amphideutopus oculatus	2.0–7.0	–	4.0	2.0–7.0	–	3.0–6.0
Batea transversa	–	–	–	3.0–4.0	1.0–5.0	2.0–4.0
Ericthonias braziliensis	1.0–6.0	–	2.0–4.0	2.0–5.0	–	2.0–4.0
Metaphoxus frequens	1.0–5.0	–	2.0–5.0	1.0–5.0	3.0	1.0–4.0

Table 5. (Continued).

Organisms present[1]	Size ranges (mm)					
	Day			Night		
	Sand	Plankton	Prey	Sand	Plankton	Prey
Monoculodes hartmanae	2.0–7.0	–	2.0–5.0	2.0–5.0	2.0–6.0	2.0–3.0
Paraphoxus heterocuspidatus	1.0–3.0	–	2.0–3.0	1.0–4.0	2.0–3.0	2.0–4.0
Photis brevipes	2.0–5.0	–	1.0–3.0	1.0–6.0	2.0–3.0	1.0–4.0
Rudilemboides stenopropodus	2.0–5.0	–	2.0–4.0	2.0–5.0	–	2.0–5.0
Synchelidium rectipalmum	1.0–7.0	–	2.0–4.0	1.0–6.0	2.0–4.0	2.0–3.0
Others	1.0–10.0	–	1.0–4.0	1.0–7.0	2.0–4.0	1.0–10.0
CAPRELLIDAE						
Caprella pilidigita	9.0	–	–	5.0–7.0	–	4.0–10.0
Mayerella banksia	3.0–5.0	–	–	2.0–5.0	–	4.0–5.0
Others	2.0–5.0	–	2.0–4.0	2.0–4.0	4.0	2.0–8.0
NATANTIA						
Larvae and juveniles	–	2.0		3.0–4.0	1.0–7.0	–
Crangon holmsi	7.0		–	7.0–11.0	5.0	5.0–12.0
Others			–	–	–	4.0–10.0
REPTANTIA						
Zoeae	–	–	–	1.0	1.0–2.0	–
Others	–	–		–	2.0–4.0	–
ECHINODERMATA						
Dendraster excentricus	5.0–14.0	–		1.0–9.0	–	–
Others	0.6–1.0			1.0–2.0	–	–
CHAETOGNATHA						
Various spp.	–	4.0–10.0		–	2.0–10.0	–
LARVACEA						
Various spp.	–	2.0–4.0	–	–	1.0–4.0	–
FISHES						
Eggs (pelagic)	–	1.0–2.0	–	–	1.0–2.0	–
Larvae	–	3.0–7.0	–	–	2.0–12.0	–
Others				–	–	–
MISCELLANEOUS	0.3–50.0	0.6	–	3.0–26.0	1.0–4.0	–

[1] See Footnote 1, Table 1.

[2] Not recorded.

forces in shaping trophic characteristics and species composition of fishes in natural communities.

Diurnal trophic interactions

Of the many fishes of varied species with access to the open sand in Ripper's Cove, only a relatively few with certain offensive and defensive abilities foraged there during the day. They included transients as well as residents. Here we consider the trophic adaptations that permitted diurnal exploitation of the prey in this habitat.

Cryptic features were adaptive for daytime activities over the open sand. This was demonstrated by the resident bothids, *Citharichthys stigmaeus* and *Paralichthys californicus*, which often compensated for the lack of environmental cover by matching their colorations to that of the substrate (Fig. 3), or by resting under a covering of sand (Fig. 4). Both species seemed to use their capacity for camouflage to ambush prey, and probably *C. stigmaeus*, the smallest species regularly observed in the study area, also used it to escape detection by predators. *P. californicus* would have had less need for protection from predators as an adult, when it is relatively large, but probably found such protection important as a juvenile.

Although cryptic features were far less evident among those fishes that moved from neighboring habitats to forage over the open sand during the day, these species had other characteristics that equipped them to seek prey there. One was the ability to detect, and capture, organisms that were highly cryptic. The way *Halichoeres semicinctus* intently inspected the substrate (Fig. 7) as it roamed about the area suggested reliance on acute vision to detect well-concealed prey. And its small mouth, with anterior canines, was suited to pluck tiny organisms from the sand. Clearly these features were adapted to exploit many of the species that we took in our samples from the environment (Tables 2 and 5). Presumably the exposed targets of *H. semicinctus* were motionless, because the organisms on which it preyed (Table 3) would be likely to avoid moving in the presence of an active predator. *H. semicinctus* apparently captured at least one major prey, the gammaridean *Photis brevipes*, by snipping off exposed tips of the tubes of the polychaete, *Spiochaetopterus costarum*, in which this amphipod lives (Table 3, footnotes 3 and 4). *Paralabrax clathratus*, on the other hand, appeared to be an opportunist that hovered, or rested, in place until nearby prey were momentarily detectable, or otherwise vulnerable. Often, it appeared that predators using this tactic depended on going unnoticed to strike at nearby organisms that drew attention to themselves by moving. *Embiotoca jacksoni* avoided the problem of detecting cryptic prey through its ability to winnow organisms from ingested sediments – a successful feeding mode in Ripper's Cove because there were so many organisms in the sand (Table 2).

When *Semicossyphus pulcher* entered the open-sand habitat from adjacent areas during the day, it foraged on some of the few potential prey that were readily visible. Despite their visibility, these prey had defenses that protected them from most fishes, if not from *S. pulcher*. Many were encased in heavy armor (e.g. the mollusk *Olivella biplicata*), but *S. pulcher* crushed them with its strong jaw teeth and pharyngeal plates. And most bivalved mollusks were buried in the sand (even though their siphons were readily visible at the surface, e.g. *Americardia biangulata*), but *S. pulcher* rooted them out with its well-developed ability to excavate. On the other hand, the many small organisms in the gut contents of even the larger *S. pulcher*, e.g. the gammarid *Ampelisca cristata* (Table 3), indicate that, like *E. jacksoni*, above, they winnowed prey from the sand and debris vented from gill and mouth openings immediately after ingestion. It is unlikely that adult *S. pulcher* could selectively ingest such tiny prey with its large mouth and heavy jaw teeth.

The four species that entered the open-sand habitat from neighboring rocks and algae probably represent a distinctive and widespread trophic category. Three of these – *P. clathratus, S. pulcher*, and *E. jacksoni* – (along with *Oxyjulis californica*, a labrid similar to *H. semicinctus*) have been reported to regularly leave kelp forests to forage in adjacent open sand at Santa Cruz Island, 100 km NW of Santa Catalina (Ebeling et al. 1980). Because they lacked the capacity for concealment so well developed in the residents, the fishes that ranged over the open sand from neighboring habitats during the day would seem vulnerable to such predators as *Paralichthys californicus*, which ambushes smaller fishes from concealed positions in the sand (Fig. 4) (Haaker 1975). But at least many of the transients, e.g. *Halichoeres semicinctus*, directed their attention at the sea floor as they foraged, and their highly developed abilities to detect cryptic organisms in the sand should also have helped them to detect, and thus evade, cryptic predators. Of those species that did not demonstrate particular abilities to detect cryptic organisms (although they may well have had such abilities), *Semicossyphus pulcher* gained some level of protection from its relatively large size, and *Embiotoca jacksoni* from its relatively deep body – both features that have been reported to reduce threats from predators (Hobson 1979).

The absence of planktivorous fishes in the water column of the study site during the day probably can be attributed to threats from predators. Although such prominent diurnal planktivores as *Chromis punctipinnis* and *Atherinops affinis* were numerous above the neighboring rocks and algae at this time (Quast 1968, Bray 1980), they did not venture above the exposed study site even though zooplankton were abundant there (Table 2). This is consistent with earlier assertions (Hobson 1968, 1979) that unacceptable risks of predation keep smaller fishes out of the more exposed regions of the water column during the day. With their attentions directed at the water column, planktivorous fishes would be especially vulnerable to predators that attack from concealed positions in the sand.

We suggest, therefore, that the relatively few fishes which foraged over the open sand of Ripper's Cove during the day were benthic feeders able to cope with the predatory threats characteristic of that habitat, and which also had either: (1) a well-developed ability to detect, and capture, species that were difficult to see, and perhaps at least partly buried, or (2) the specialized capacity to take forms that, while more visible and exposed, were heavily armored.

Nocturnal trophic interactions

The sharp increase in numbers of fishes that foraged in the open-sand habitat at night – most of them after migrating from daytime shelters elsewhere – indicated nocturnal relaxation of the constraints that limited fishes' access to that habitat during the day. Diel migrations between diurnal shelter sites and exposed nocturnal feeding grounds are widespread among nearshore fishes (Hobson 1968, 1973, McFarland et al. 1979), and appear based on two developments on the exposed feeding grounds at night: prey become more accessible, and predators become less threatening.

Much of the difference in trophic relations from day to night can be attributed to diel differences in visual capabilities. In bright light the visual systems of most nearshore fishes stress visual acuity, but in dim light visual acuity is sacrificed for visual sensitivity (Walls 1942, Munz & McFarland 1973). So at night the fishes lose much of their ability to target smaller organisms, and probably at least many sense only those prey that move. Certainly at night there is less need among both predators and prey for the cryptic features that are so adaptive by day.

With the nocturnal loss of visual acuity in fishes removing many of the threats that kept smaller organisms hidden in the sand during the day, many potential prey (e.g. various mysids, tanaids, isopods, and amphipods) became active in exposed locations, including the water column. For every organism of a predominantly benthic species that entered the nocturnal water column, however, many more of the same species remained in the sand (Table 2). So the numbers that came under threat from nocturnal planktivores were relatively few compared to the numbers of conspecifics still on the bottom that remained threatened by nocturnal benthivores. For example, while the tubiculous amphipod *Ampelisca cristata* recurred in the diet of the strictly planktivorous and nocturnal *Hyperprosopon argenteum*, it was far more numerous in the diet of the strictly benthivorous, and nocturnal, *Umbrina roncador*.

Most of the fishes that foraged in the open-sand habitat at night captured their prey in, on, or close to the sand, and they showed their suitability for this task by capturing representatives of virtually every species present – except the sedentary, armored mollusks and echinoids. The absence of sedentary forms from their diet is consistent with earlier assertions that prey must move to be effective targets for at least most nocturnal predators (e.g. Hobson 1979).

At night the fishes seemed to hunt more effectively on the open sand than among the neighboring rocks and algae. Probably prey not only were more accessible in the exposed habitat, but also more visible due to moonlight and starlight reflected from this light substrate (Hobson et al. 1981). Thus, elevated light levels over sand at night may account for the presence and predatory success there of the predominantly diurnal, subadult *Paralabrax clathratus*. Some of the nocturnal fishes in this habitat, however, may not have depended on vision to capture prey. For example, *Chilara taylori* apparently detected prey with its barbel-like pelvic fins (Fig. 9), just as the closely related *Otophidium scrippsi* has been reported to do (Greenfield 1969). Probably *Umbrina roncador* used the single short barbel at the tip of its lower jaw (Fig. 12) in a similar way.

The only fish species that regularly foraged more than 2 m above the sand in the study area at night was *Hyperprosopon argenteum*. This species fed almost entirely on the primarily benthic crustaceans that entered the water column after dark, even though these were only a small minority of the nocturnal plankton (Table 2). Certainly these prey made better nocturnal targets than did the far more abundant holoplankters, which probably were too small or transparent to be effectively seen in dim light. Not only were the crustaceans that entered the water column at night generally much larger and more opaque than the holoplankters, many were awkward swimmers (e.g. caprellids), and therefore less elusive, and also more likely to create the turbulence and resulting bioluminescence that is thought to direct many nocturnal attacks (Hobson et al. 1981). Significantly, *H. argenteum* as small as 44 mm SL (unpublished data collected elsewhere) similarly fed on these same crustaceans, especially gammarids and caprellids, rather than on the more numerous, but smaller and less visible holoplankters.

We make two inferences from the exceptionally large eyes of *H. argenteum* (Fig. 10): first, that it hunted visually, and second, that there was less light in the mid regions of the water column, where it foraged, than in the lower regions of the water column, close to the sand, where related fishes with smaller eyes, e.g. *Cymatogaster aggregata*, captured similar prey (Table 4, Fig. 11).

Nocturnal planktivores may find foraging less productive above the open sand than above neighboring rocks and algae, which reverses the situation involving benthivores, described above. While benthivores seemed to find the open-sand habitat more favorable because of higher light levels, and more accessible prey, the planktivores would have found prey more diverse and abundant above rocks and algae. Apparently the number and diversity of benthic organisms that entered the water column at night reflected the relative complexity of their benthic habitats. Thus, at night zooplankters were fewer in kind and number above the sand in Ripper's Cove than above more complex fields of benthic algae in Fishermen's Cove, 9 km away (Hobson & Chess 1976). And this difference in the numbers and diversity of nocturnal zooplankters may have influenced the numbers and diversity of planktivorous fishes, because while just *H. argenteum* foraged regularly above the open sand in Ripper's Cove at night, five planktivorous species foraged regularly above the fields of benthic algae in Fishermen's Cove after dark (Hobson & Chess 1976).

The visual limitations of nocturnal predators that reduced threats to smaller benthic invertebrates at night should also have reduced nocturnal threats to smaller fishes. But as with benthic invertebrates, the safety would have been only relative. At least one piscivorous ambusher that frequents the open-sand environment at Santa Catalina Island – the angel shark, *Squatina californica* – is most active at night (Standora & Nelson 1977). *S. californica* feeds primarily on active fishes (Limbaugh 1955), which it attacks by lashing upward from a position at rest on the sand (Pleshner 1983). At least many of its nocturnal strikes may be directed by a bioelectric sense – a capability widely developed among elasmobranchs (Kalmijn 1971). *S. californica* prefers depths of about 20 m (Limbaugh 1955), but occurs shoreward to the water's edge (Pleshner 1983). So while we did not see this shark in Ripper's Cove, it co-occurs with the fish species considered here over much of their ranges (Miller & Lea 1972), and so is likely to have influenced the evolution of their defenses. Furthermore, although the piscivorous *Paralichthys californicus* has been reported to feed mainly by day (Haaker 1975), we would expect its ambushing tactics to be successful under at least some nocturnal circumstances. There may be enough light from moon or stars to direct some attacks, and on even the darkest nights certain targets may be suitably marked by bioluminescence (Hobson et al. 1981).

The impact of predator-prey interactions on trophic features and community structure

Clearly, the variety of form and habit in fishes that foraged over the open sand of Ripper's Cove was closely related to the variety of form and habit in their prey. But many fishes with access to that habitat, and capable of exploiting its inhabitants, e.g. the diurnal planktivores, did not do so, probably because they lacked means to evade the predators there. Thus, the fish species present in the open-sand habitat were characterized by a combination of morphological and behavioral characteristics which enabled them to both capture prey and evade predators under the circumstances that prevailed in that setting.

A species can be defined by a combination of morphological and behavioral features adapted to its specific mode of life, and certainly among the more prominent of these features are the means to capture prey, or to thwart predators. These relationships are evident in even the most casual appraisal of trophic characteristics and of course the distribution of morphological and behavioral types among individuals that live together is the basis of their community structure. But while it is recognized that trophic relationships are important forces in structuring animal communities, a prevailing view identifies the primary mechanism as competition between predators for prey (e.g. MacArthur 1972, Moermond 1979, Hixon 1980, Larson 1980). Generally this view recognizes predation as important, but usually in the sense that it modifies patterns of competition (for space, as well as food: Paine 1966, Pianka 1974, Connell 1975, Roughgarden & Feldman 1975). In fact, until recent criticism (e.g. Lewin 1983), the concept of competition as the major force determining the structure of animal communities had become so firmly entrenched in ecological thought as to approach dogma (Wiens 1977).

The impact of interspecific competition for food on trophic features of fishes, and on the species composition of fish communities, would seem to have been greatly overstated. This is true even where forceful competition for food is on occasion likely, as where the interacting elements are locked together in lakes, streams or other closed ecosystems. (The strongest evidence of competitive trophic interactions affecting ecological relationships comes from closed systems, e.g. Johannes & Larkin 1961). Often in such situations it has been asserted as simple statement of fact that interspecific differences in trophic characteristics reduce competition, and generally there are inferences that the advantage of reduced competition for food has been the major selective advantage of these characteristics. In their classic study of fishes, for example, Keast & Webb (1968, p. 1845) stated, without benefit of supporting evidence, that '... mouth and body structures combined with food specializations ... to greatly reduce interspecific competition'. And, in reference to birds, Cody (1974, p. 87) stated '... the variety of feeding methods is necessary to allow coexistence' (by reducing competition). Although distinctive trophic features reduce the chance of interspecific competition, we suggest that in most cases this reduced competition is simply an incidental result of evolutionary processes driven primarily by interactions between predators and prey. This view agrees with Connell (1980), who, in questioning the importance of competition in community structure, was of the opinion that species divergence leading to niche separation is more likely to result from interactions (coevolution) between two species on different trophic levels than between two species competing on the same trophic level.

Certainly there can be little doubt that trophic characteristics in fishes are largely products of interactions between predators and prey. Furthermore, the evolution of feeding adaptations in predators is inseparable from the evolution of defensive adaptations in prey. As stated earlier (Hobson 1979, p. 231): 'Attacks by ... predators during the evolution of modern species have pressured prey to acquire effective defensive adaptations. But every successful defense has evoked an appropriate offense, so that a delicate balance now exists.' This balance between predator and prey, based on a system of coevolved offenses and defenses, should be a stabilizing influence on community structure. But while the usual condition of balanced predator-prey relationships should establish relative stability, it nevertheless involves intense conflicts between predator and prey which continue to refine the distinctive trophic features that distinguish the species.

Thus, the fishes of Ripper's Cove were distinguished by morphologies and behaviors that would seem adaptive responses to the defensive structures or tactics of their prey. *Semicossyphus* *pulcher*, for example, was characterized by being strongly diurnal, by having heavy pharyngeal teeth, and by a highly refined ability to excavate organisms from the sediments. These features provided visual conditions and capabilities suited to detect, capture, and digest its major prey – armored organisms that were motionless and at least partially buried in the sand. Similarly, *Hyperprosopon argenteum* was characterized by exceptionally large eyes and nocturnal habits, which were adaptive in feeding on organisms that entered the water column only under cover of darkness. Obviously these distinctive characteristics are products of evolutionary processes that greatly transcend interspecific encounters in any single environment. The specialized dentition of *Semicossyphus pulcher,* for example, adapted this species over its geographic range to crush a greater variety of armored prey than occurred in the limited setting of our study area. So the combination of fishes that occurred in Ripper's Cove during the present study was, in effect, a mix of species with access to that habitat that were able to exploit the prey, and to tolerate the predators, that existed there at that time.

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A Small Vessel Technique for Tracking Pelagic Fish

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ABSTRACT—Tracking of pelagic fish has previously been conducted from large research or fishing vessels, both of which are expensive to operate. We have adapted advances in ultrasonic tracking technology to permit tracking of pelagic fish from a small (33-foot) vessel. Sportfishing techniques have been successfully employed to capture fish for tracking.

The use of a small vessel has many advantages including maneuverability in congested areas, the ability to work both offshore and close to shore, high responsiveness to changes in fish behavior, and low operating costs. Low operating costs allow the vessel to be utilized over extended periods, thereby permitting replication of experiments. High quality data on the vertical and horizontal movements of pelagic fish have been acquired for periods of up to 6 days. These techniques could be utilized to track fish inexpensively in a wide range of locations.

Introduction

The advent of ultrasonic telemetry techniques for monitoring fish movements in the wild has greatly increased our understanding of the behavior and physiological capabilities of pelagic fish (Carey, 1983). The development of pressure sensitive transmitters has allowed insights into the remarkable pressure (depth) and temperature tolerances of these animals while simultaneously revealing their fine-scale horizontal movements.

Previous tracking studies involving pelagic species have been carried out using large fishing or oceanographic research vessels. Because of the high operating costs of these vessels and the heavy demands on their time, comparatively few fish have been tracked. Also, the tracks that have been made come from widely scattered areas. Thus, although valuable data have been acquired from individuals of several species, only rarely have enough replicate tracks been obtained to give a reasonable indication of the normal daily behavior of a species in a particular location. Pelagic species that have been tracked include skipjack tuna, *Euthynnus pelamis* (Yuen, 1970); yellowfin tuna, *Thunnus albacares* (Carey and Olson, 1982); albacore, *T. alalunga* (Laurs et al., 1977); swordfish, *Xiphias gladius* (Carey and Robison, 1981); blue marlin, *Makaira nigricans* (Yuen et al., 1974); mackerel sharks (Carey et al., 1981); and Atlantic salmon, *Salmo salar* (Westerberg, 1982).

This paper reports on the development of a technique for using a small vessel for the ultrasonic tracking of pelagic fish. Our system produces high-resolution data and is sufficiently adaptable and cost-effective to allow prolonged tracking efforts in a variety of situations. Because of its modest cost, a small vessel can be dedicated to a tracking project for extended periods. This permits acquisition of many replicate multi-day tracks. Thus, sufficient amounts of data can be acquired to yield reliable information about the sequential daily behavior of a target species. Details of our system and methods have been included to allow other workers to adapt our techniques to their own needs.

The impetus for development of our tracking technique began when the Honolulu Laboratory of the National Marine Fisheries Service (NMFS) Southwest Fisheries Center pioneered the modern use of fish aggregating devices (FAD's) by deploying several of these buoys in Hawaiian waters in 1975 (Matsumoto et al., 1981). These deep-water FAD's have proved to be very effective and their use has spread throughout the Indo-Pacific (Shomura and Matsumoto, 1982). However, the influences of FAD's on fish behavior which result in the aggregation of pelagic fishes at these buoys are not understood. Given the importance of FAD's, the high costs associated with FAD deployment, and unanswered questions relating to stock harvesting and management, we initiated a project using ultrasonic transmitters and a small pursuit vessel to document the movements of pelagic species associated with FAD's. To date, our efforts have concentrated solely on yellowfin tuna and bigeye tuna, *T. obesus*, with fork lengths between 50 and 75 cm.

Methods

General

Our two major objectives when equipping the vessel were simplicity and redundancy. The data acquisition and recording systems were designed to emphasize shore-side data processing,

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thereby maximizing the use of on-board space and equipment for actual acquisition and storage of high-quality raw data. Secondary objectives were minimizing operating costs and maximizing crew comfort, thus improving our ability to track fish for long durations.

The Vessel

The R/V *Kaahele'ale* is a 33-foot vessel built for the U.S. Navy as a personnel boat. It was acquired by the NMFS in 1979 and modified for nearshore fisheries research, primarily telemetry. As modified, the vessel has an open-stern deck, a semi-enclosed central cabin with engine beneath, and a fully enclosed forward cabin. The stern deck is equipped for fishing and tagging. The central cabin houses the steering console and an instrument rack containing the telemetry equipment, navigation equipment, and radar. The forward cabin is air conditioned and contains two bunks, a work bench, an expendable bathythermograph (XBT) system, and a microwave oven.

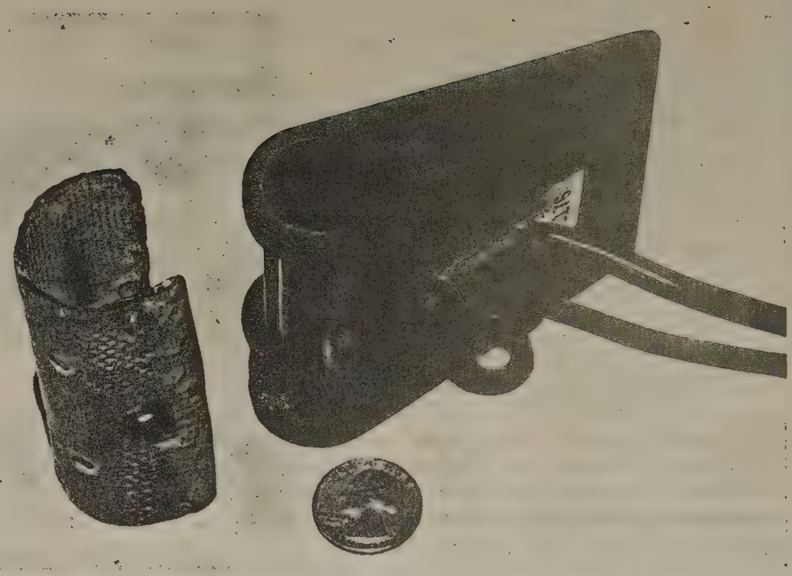
Figure 1.—The directional hydrophone is shown with fiberglass faring removed. Holes in the faring permit attachment to hydrophone body and allow water to flood the space between the hydrophone and the faring. The hydrophone sideplate has been removed to show hydrophone and preamplifier.

The vessel is powered by a single screw driven by a GM-671[1] diesel engine through an Allison hydraulic transmission. Two 120-gallon fuel tanks are backed with a 50-gallon reserve tank. At cruising speed (11 knots), fuel consumption is 10 gallons/hour, at trolling speed (7.5 knots) it is 5 gallons/hour, and during tracking operations fuel consumption is usually less than 3 gallons/hour. The main engine alternator supplies a 24 volt main battery which powers the starter motor, the radar, and autopilot. Radios, tracking instrumentation, navigation lights, and fathometers are powered by a separate 12V DC battery bank. A 7.5 KW 120V AC diesel generator (Onan) is housed below a portion of the stern deck and powers the XBT system, the microwave oven, the forward cabin air conditioner, and an automatic 12V battery charger.

Tracking Apparatus

Transmitters

Pressure sensitive 50 KHz ultrasound transmitters were purchased from Vemco, Halifax, Nova Scotia. Two types of transmitters have been used, one with an expected operation life of up to 22 days and the other with nominal expected life of 3 days. We have found maximum open ocean operating ranges to be about 0.8 miles for the 3-day tags, and about 0.5 miles for the 22-day tags. The transmitters are pressure sensitive such that the pulse frequency of the 50 KHz carrier signal is directly proportional to increasing pressure (depth). Normal operating range is zero (surface) to 500 psi (370 m depth). The 22-day duration transmitters are cylindrical (8.0 cm long and 1.6 cm diameter) and weigh 27.7 g in air and 11.7 g in seawater. The 3-day duration transmitters are of similar specifications. The transmitters are equipped with magnetically operated reed switches for rapid activation and have a nylon loop at one end for use in attachment to the fish (discussed later).

Receivers

The 12V DC amplifier/receivers (CR-40, CAI Co.) are matched to the transmitters with 50 KHz crystal-controlled oscillators. These receivers amplify and convert the telemetered pulses into an audible signal. Two receivers were installed on the vessel in case one of the units failed during a track.

Hydrophone

The directional hydrophones were also manufactured by Vemco. However, a small but very significant modification was made after delivery from the factory. This modification involved the fabrication and installation of a 2 mm thick fiberglass faring over the leading face of the hydrophone (Fig. 1). This faring serves to protect the actual sensor from physical damage and, more importantly, reduces noise generated by water passing over the hydrophone. The signal/noise ratio is improved to such an extent that usable data can be acquired at boat speeds in excess of 7 knots. We can therefore track and acquire depth data from fast moving fish. The faring also allows the boat to be driven at 11 knots without damage to the hydrophone. No reduction in operating range

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[1] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

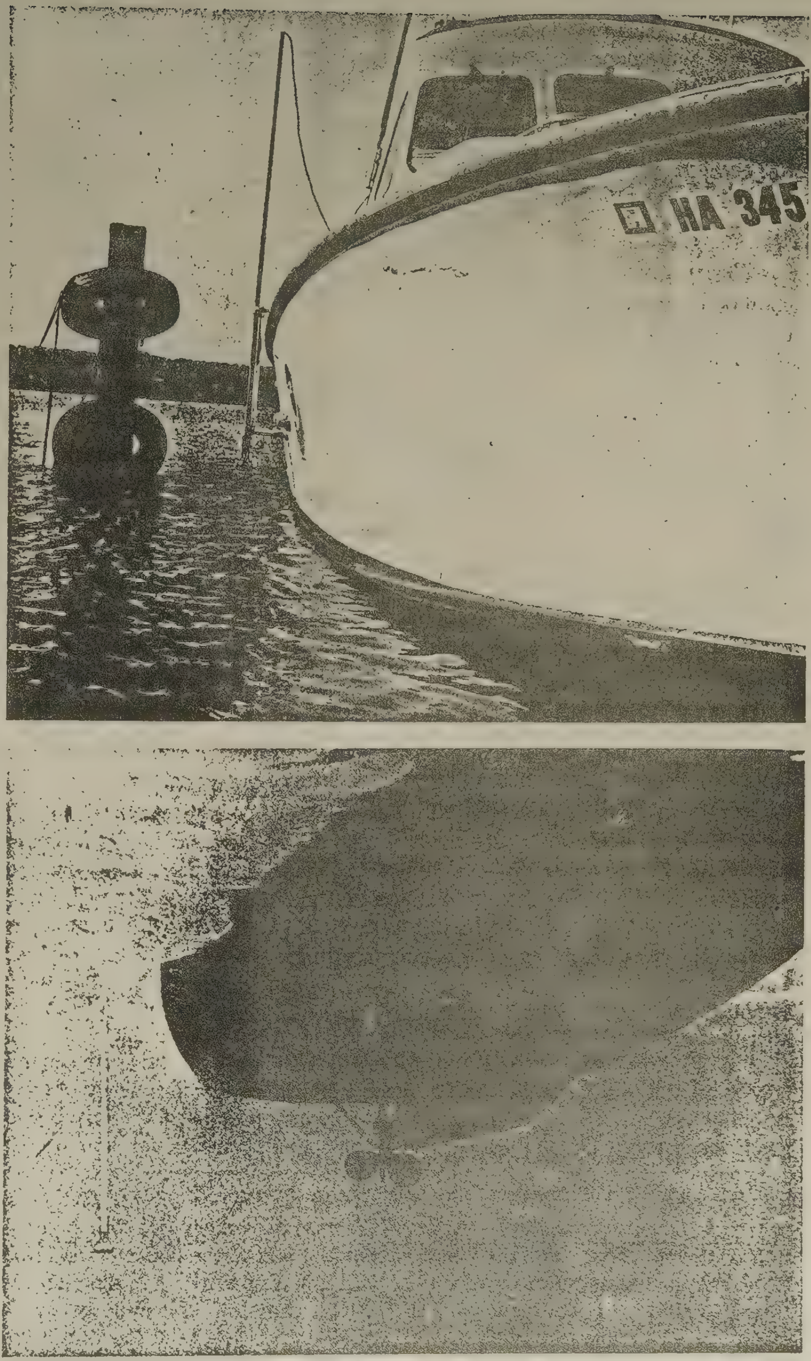

Figure 2.—Hydrophone Mounting. Top: The tracking hydrophone is in retracted position. Two triangular aluminum brackets mounted above the waterline allow the hydrophone to be lifted out of the water when not in use. Bottom: The hydrophone mounting pole is lowered through the support brackets to a position in which the hydrophone is clear of the keel and is unaffected by turbulence from the boat hull.

was observed following installation of the faring.

The hydrophone is braced within a stainless steel bracket bolted to the end of a 10-foot length of 1-inch I.D. galvanized pipe. The shielded cable from the hydrophone to the amplifier is threaded through the pipe. Shielding the cable is necessary to reduce radio frequency interference.

The hydrophone mounting pipe is deployed amidships using two triangular brackets, constructed of 1-inch I.D. aluminum tubing, which are bolted, one above the other, through the hull above the waterline. The pole is free to slide through the brackets and is held in place by thumbscrews. Thus, the hydrophone can be lowered for tracking and raised out of the water when not in use. This outrigger type of mounting allows the hydrophone to run about 5 feet below the surface and 6 feet to the side of the keel where it is unaffected by water turbulence generated by the hull (Fig. 2). During tracking, the hydrophone is secured facing forward in parallel with the keel of the boat, and localizing the transmitter (i.e., the fish) is accomplished by turning the vessel.

Depth Data Logging

A data processor/frequency counter (Telonics, TDP-2) is connected to the audio output of the receiver. This processor unit provides a digital display of the inter-pulse interval which is recorded manually at regular intervals and which gives an immediate indication of the fish depth and any changes in behavior. A cassette tape recorder is also connected to the audio output of the receiver. This provides a continuous record of the telemetered depth data for fine-scale plotting and analysis ashore.

Navigation

Three types of fixes are used to determine the vessel's position during tracking. The primary navigational reference is by Loran C (Furuno LC-80). This unit provides latitude and longitude in-

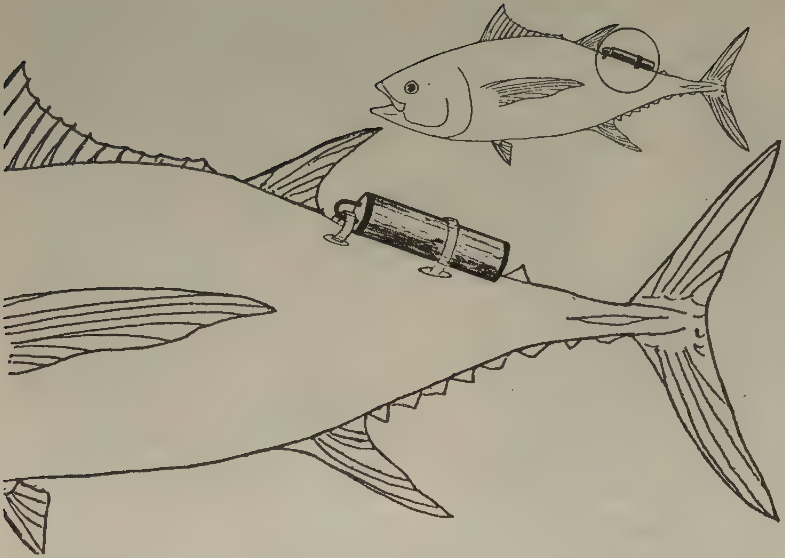

Figure 3.—The ultrasonic transmitter is attached to the dorsal surface using two nylon tiewraps inserted through the dorsal musculature and pterygiophores.

formation and also the vessel's course and speed. These latter data are useful in subsequent onshore analysis of the fine-scale movements of the fish. The waypoint storage capability of this unit also permits instantaneous information about the vessel's current position relative to starting or other important (e.g. FAD) positions. Supplementary visual fixes on charted landmarks are made using a hand-bearing compass or sextant. These visual fixes are made hourly to ensure the accuracy of the Loran C positions. The 24V DC radar unit is used to acquire accurate distances to landmarks or FAD's.

Oceanographic Information

Knowledge of the thermal structure of the ocean is essential to interpretation of the movements of the fish. Temperature data are acquired using a 110V AC expendable bathythermograph (XBT) system (Sippicon, Mass.). The XBT probes are deployed about every 3 hours or whenever the fish being followed moves into new waters (e.g., onshore to offshore). A bucket thermometer is used to verify the accuracy of the XBT surface temperatures.

Water current direction at FAD locations is determined by visual inspection of plastic streamers attached to the FAD's mooring chain. When operating in inshore areas (<100 fathoms) a fathometer is used to record ocean depth and to assist in determining geographic position.

Fishing and Tagging Techniques

The research vessel is equipped for both handline (drift) fishing and trolling. To date, most fish have been caught trolling. Artificial trolling lures tailored to the size of the target species are used with single "J"-type hooks. Large reels (14/0, Penn Reels, Pennsylvania) and 130-pound test line are used so that the fish can be reeled in rapidly to reduce capture stress. The reels are set with very light drag to reduce injury to the fish's mouth. After the initial strike and run, the drags are tightened and the fish brought to the boat as quickly as possible. Occasionally, the fish are towed behind the slowly moving vessel while the remaining fishing gear is retrieved and the stern deck prepared for tagging.

The tagging cradle is located in the center of the transom. The cradle is a foam-lined, "V"-shaped trough with one side hinged to allow variable gape to accommodate fish of different sizes. The fish to be tagged is lifted aboard, lightly wedged into the cradle and its eyes covered with a wet chamois cloth. These procedures are usually sufficient to immobilize the fish. Once aboard, species identification is verified, the hook removed, and mouth damage assessed and the fish length measured. Handling is performed without gloves which remove large amounts of mucus from the fish's surface.

Using the nylon loop embedded in one end of each transmitter, the unit is attached to the dorsal surface of the fish (adjacent to the second dorsal fin) using nylon "tie-wraps." These are inserted through the dorsal pterygiophores using sharpened hollow brass needles. Two tiewraps are used per fish; one passing through the transmitter loop, the other half way along the transmitter's length to prevent the transmitter from wobbling from side to side. After insertion through the musculature, the tie-wraps are cinched down and trimmed (Fig. 3). The fish is then released. The entire operation requires the fish to be on board between 1 and 2 minutes.

Tracking Techniques

Testing of the transmitter/receiver system has demonstrated that maximum operational range is between 0.25 and 0.8 n.mi., depending on the type of transmitter being used. Furthermore, we have established that maximum deflection of the signal amplitude meter on the CAI receiver occurs when the transmitter is within about 200 m of the vessel. Consequently, during tracking we attempt to keep the fish at just the distance where maximum gauge deflection occurs. This gives us added confidence in the accuracy of our tracks and also that we are not unduly "crowding" the fish. The directional hydrophone (and therefore the boat) is kept pointed at the fish by maximizing the audio output of the receiver. The small size of the vessel permits rapid changes of direction and rapid identification of the direction of the signal. Due to the noise reduction resulting from the installation of the hydrophone faring, a fish can be pursued at up to 7 knots if it appears to be drawing away. At higher pursuit speeds depth data recording must be temporarily suspended because the noise of water rushing past the hydrophone masks the transmitter's signal.

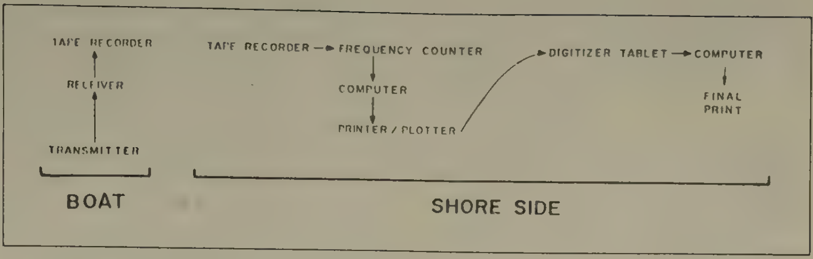

Figure 4.—Schematic representation of the data acquisition and analysis process.

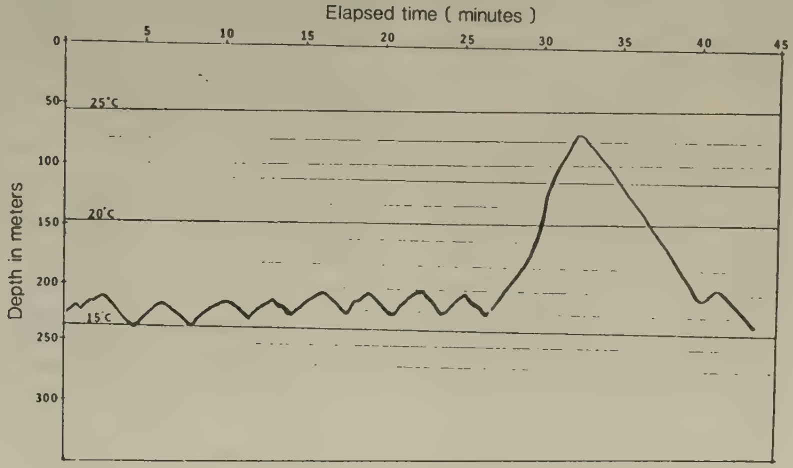

Figure 5.—A 45-minute vertical movement plot. Continuous recording of vertical movement data on cassette tapes allows both fine-scale and large phenomena to be discerned. Superimposing XBT data indicates that the swimming depth of this bigeye tuna is strongly influenced by the 15° and 17° C isotherms. Depth data of this type are recorded for the entire duration of each track.

Data Acquisition

During tracking, four types of data are acquired: 1) A continuous tape of fish-depth data from the audio output of the CAI receiver, 2) water depth/temperature profiles (XBT), 3) water depth, and 4) navigational data. Navigational data are recorded every 10 minutes and include: 1) Time, 2) heading/engine RPM, 3) Loran C fixes, and 4) visual and radar fixes (usually taken hourly). When close enough to a FAD, its range and bearing from the vessel are also recorded every 10 minutes. A narrative commentary is compiled to assist in subsequent data analysis.

Data Analysis

Vertical Data

Figure 4 summarizes the system for acquisition and analysis of vertical movement data. Once ashore, the recorded information is played from the cassettes into a Telonics TDP2 Data Processor. This processor is modified to output a +5V DC square wave each time a sound pulse is detected. A Hewlett Packard (HP) frequency counter (HP5308A) is used to time every other pulse interval. An HP 9845 computer with real-time clock converts the pulse intervals to depth and plots a graph of depth versus elapsed time. This original hard copy of the fish's swimming depth contains some erroneous points which are eliminated by tracing the depth-time profile on an Apple computer digitizer pad. This "cleaned" track (where depth is plotted every 10 seconds) is then stored on floppy disks prior to final plotting and analysis. Bathythermograph temperature profiles are superimposed on the final printouts (Fig. 5).

Horizontal (Position) Plotting

Because of the proximity of the tracking vessel to the target fish, no attempt is made to distinguish between the positions of the two. Plots are made on navigation and bathymetry charts based on Loran C positions recorded manually at sea. These relative positions are checked against the visual and radar fixes that were concurrently collected. Where applicable, fathometer readings are used as cross references for the other navigational data. Fine-scale movements of fish in the immediate vicinity of FAD's are plotted using manual records of the buoy's range and distance relative to the vessel.

Results

Since the installation of the tracking equipment in its current form, we have acquired 11 tracks of yellowfin tuna and 2 tracks of bigeye tuna that were caught near FAD's or near the adjacent coastline. The duration of the tracks ranged from 8 hours to 6 days.

All but one of the fish was caught by trolling. The small (6/0) size of hooks and light drag settings result in comparatively minor hook wounds. In only one instance has a fish died immediately upon release. All others have shown rapid recoveries to, what we believe, based on consistency within and across samples, is normal behavior. None of these tracks have been terminated due

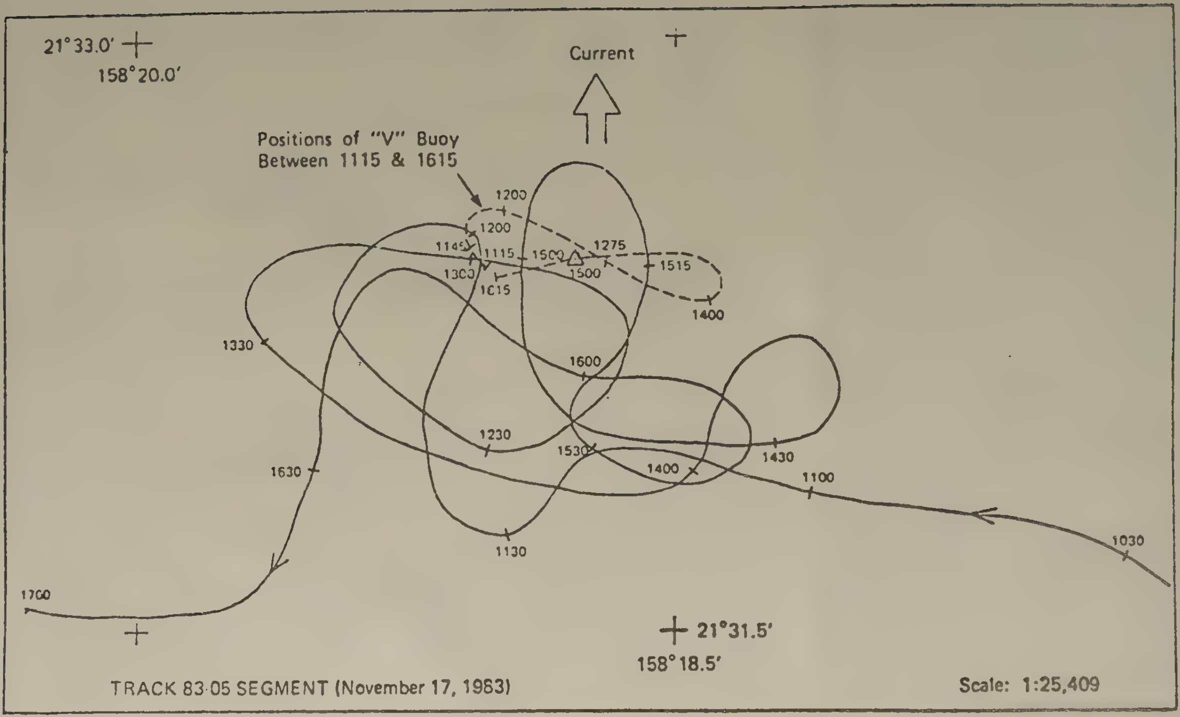

Figure 6.—Fine-scale horizontal plotting. Loran C, radar, and visual fixes allow fine-scale movements to be plotted. After arriving at FAD "V" off of Waianae, Oahu, this 55 cm yellowfin tuna spent about 85 percent of the next 5 hours on the upcurrent side of the buoy. The "Figure 8" movement of the buoy can also be plotted.

to death of the fish.

Captive fish tagged with the "double tie-wrap" method and observed in large tanks at the Kewalo Research Facility of the NMFS Honolulu Laboratory were able to swim normally with the school and appeared healthy after the 2-week observation period ended. In addition, a fortuitous recovery of a tagged fish by a fisherman attests to the suitability of our trolling/tagging technique. This fish was caught by a fisherman trolling near a FAD 3 weeks after we obtained a 36 hour track of it.

Discussion

Although almost all of the technology incorporated in the current research had been previously developed and utilized by others, we feel we have made significant advances in successfully adapting these techniques to a small vessel. Also, the ability to chase pelagic, highly mobile fish at 7 knots in the open ocean and still simultaneously collect vertical movement data is an innovation. We believe that our cassette recording and subsequent plotting of the vertical movement data has produced higher resolution vertical movement data than have previously been published. The continuous depth record has revealed phenomena (such as rapid vertical excursions and small scale oscillations) that manually collected data would have missed (Fig. 5). When the XBT data are superimposed on the tracks, much of the vertical behavior shows correlations with temperature (Fig. 5). Similar temperature influenced behaviors have been observed in bluefin tuna, *Thunnus thynnus* (Carey and Olsen, 1982).

The Loran C system of geographic plotting, when referenced with visual fixes, provides high resolution positioning of both large- and small-scale movements (Fig. 6). When Loran information is used in conjunction with visual fixes and radar ranges, small-scale movements of both the fish and FAD's can be plotted. Knowledge of the relationship between signal amplitude and transmitter distance lends confidence to the precision of the small-scale plots.

The small size of the tracking vessel has proved to have several advantages. For example, while able to pursue fish in the open ocean, the maneuverability of the vessel has also permitted unobtrusive data collection even when in the midst of many other vessels fishing at the FAD locations. Also, fish have been tracked to within 200 m of shore where larger vessels could not safely go. Similar situations occur in other locations such as straits, bays, lakes, and estuaries where tracking studies might be worthwhile but where large vessels would be too cumbersome. A vessel such as ours is capable of continuously following a fish both when it is moving in inshore (e.g., estuarine) waters and also when it moves offshore where it would be beyond the range of fixed hydrophone arrays or of very small vessels such as skiffs.

Of course, small vessels are not suitable for mid-ocean work or offshore locations beyond refueling range. However, they could be used very successfully in association with a larger mother ship which could be performing other tasks while the small pursuit vessel was tracking.

The comparatively low hydrodynamic and mechanical noise generated by our small hull allowed the hydrophone to be attached directly to the side of the boat, thereby precluding the need for complex towed arrays such as have been deployed in some other tracking studies which used large vessels. Similarly, because a small vessel is very maneuverable and can accelerate quickly, the hydrophone can be permanently locked in an orientation parallel with the keel and the entire boat turned to accomplish maintaining contact with the target fish. This high responsiveness eliminates the need for rotatable or multi-head hydrophone systems such as have sometimes been used in the past.

Much of our tracking work has been conducted out of small boat harbors with depths of 2 fathoms or less and which would have been inaccessible to larger fishery research vessels. Each 24 hours of tracking consumes about 70 gallons of fuel. At this rate our vessel can track for at least 3 days without refueling, which can be conducted at any nearby small boat harbor. We have found crews of three sufficient for all phases of the field work. This, combined with the low fuel costs, makes the total operating cost of each tracking expedition extremely modest when compared with the $5,000 to $15,000 daily costs of large research vessels or commercial fishing boats. Our modest expenses enable the vessel to be dedicated to the tracking project for extended periods. This allows replicate tracks of different species from various locations. Also, because the vessel is committed to the tracking project full time, we can take advantage of short term increases in fish abundance and avoid fishing when fish are not abundant. Our ability to use sport fishing techniques to obtain fish for tracking indicates that labor-intensive trapping methods or expensive bait-boat techniques are not obligatory for a successful tracking program.

The small size and modular nature of the actual tracking equipment is such that it could be quickly installed on almost any suitable vessel. The major installation requirement is the bracing of the hydrophone brackets to the hull. However, since the bracket mountings are well above the water line, even this aspect of the installation could easily be repaired when the tracking is completed. The availability of an AC power generator has proved to be essential. Not only does this provide XBT capabilities but also allows improvement in crew facilities such as hot food and air conditioning.

The two major limitations of our system are fuel capacity and crew fatigue. We have solved the former by refuelling during prolonged tracks. However, this technique may be unique to our project because of the proximity of small boat harbors and the rhythmicity of behavior of some of our fish which has allowed us to relocate them after temporary suspension of tracking. Crew fatigue is inevitable with a small vessel after a few days on water. We feel that in our case this could be substantially remedied by using only a slightly larger vessel (e.g., 40-45 ft) which would be somewhat more spacious and comfortable and yet which would retain the desirable characteristics of maneuverability and low operating costs. Another possible technique would be the use of a shuttle vessel to exchange crews on the pursuit vessel.

We are currently unable to be completely sure whether or not the fish being tracked is travelling alone or in a school. We feel this shortcoming will be rectified by the installation of a chromoscopic fish finder.

In general terms, however, we feel that we have developed a cost-effective technique for acquiring high-quality tracking data which could be adapted to a range of small vessels operating in a variety of situations and locations. This, in turn, will result in a significant increase in our understanding of the normal behavior of commercially important fish species about which not much is currently known. Such an increase in our understanding will improve both management and fishing techniques.

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8637

ACANTHURIDAE — Kala

by Victor A. Honda

Valid name	*Naso unicornis* (Forsskål 1775) (Fig. 70)
Synonymy	*Chaetodon unicornis* Forsskål 1775 *Monoceros biaculeatus* Bloch and Schneider 1801 *Monoceros raii* Bloch and Schneider 1801 *Naso fronticornis* Lacepède 1802 *Aspisurus unicornis* Rüppell 1828 *Naseus fronticornis* Cuvier and Valenciennes 1835 *Naseus olivaceus* Cuvier and Valenciennes 1835 *Harpurus monoceros* Foster and Lichtenstein 1844 *Priodon anginosus* Bleeker 1854 *Naseus unicornis* Günther 1861 *Monoceros marginatus* Seale 1901 *Acanthurus unicornis* Jordan and Evermann 1905 *Naseus* (*tapeinosoma* ?) Weber 1913 *Monoceros unicornis* Barnard 1925 *Prionolepis hewitti* Smith 1935 (from De Beaufort and Chapman 1951)
Common and vernacular names	Surgeonfish; unicornfish; long-snouted unicornfish; kala

Distribution

Occurs throughout the main islands. Present on all islands in the NWHI from Nihoa to Kure Atoll (Okamoto and Kawamoto 1980) and Bank 8 (JAMARC 1973). Inhabits subsurge areas (about 30 m) of moderate to dense coral growth, including fringing reefs, deepwater reef patches, reef filled bays, and coral rich parts of the lagoon (Jones 1968).

Distinguishing characteristics

D. V-VI, 27-31; A. II, 26-30; Gr. 4+9 (Masuda et al. 1975). Body short, deep, compressed, elevated anteriorly, highest at beginning of dorsal fin; snout pointed, usually projecting beyond frontal horn; horn projecting forward and downward from the preopercular region, varying greatly with age, most prominent in adult and scarcely developed in young; teeth small, bluntly pointed canines not serrated, close set, slightly recurved; short, nearly vertical shallow groove anterior to eye below nostrils. Origin of dorsal over upper end of gill opening; dorsal spines strong, rough, the first two in head, others successively short; dorsal ray slender, weak; origin of anal under base of sixth dorsal spine; anal spines and rays short; caudal deeply lunate; skin uniform, rough velvety; caudal peduncle with two low spiniferous plates on each side (Jordan and Evermann 1905).

In life, dirty olive, paler below; top of head and horn dark olivaceous; caudal spines pale blue; dorsal fin pale blue, crossed by six narrow pale yellow lines curving upward and backward, edge of fin narrowly blue; anal similarly marked.

Life history

Juveniles have rows of dark spots on a light-colored body. At about 12 cm SL, the horn becomes evident. Metamorphosis takes place at about 65 mm SL and the young are occasionally caught in tide pools (Gosline and Brock 1960). The lunate caudal fin of the adult undergoes a change with growth as the upper lobe elongates into a filament (Aoyagi 1943). Kala, a browser, is a true herbivore. It feeds by biting and tearing off bits of multicellular benthic algae without ingesting any of the inorganic substrate (Jones 1968).

Gear and catch

Kala is taken mainly by gill nets; traps and bag nets contribute smaller amounts. In 1961-79, the annual commercial catch of kala varied between 5,878 and 17,799 kg and averaged 10,081 kg.

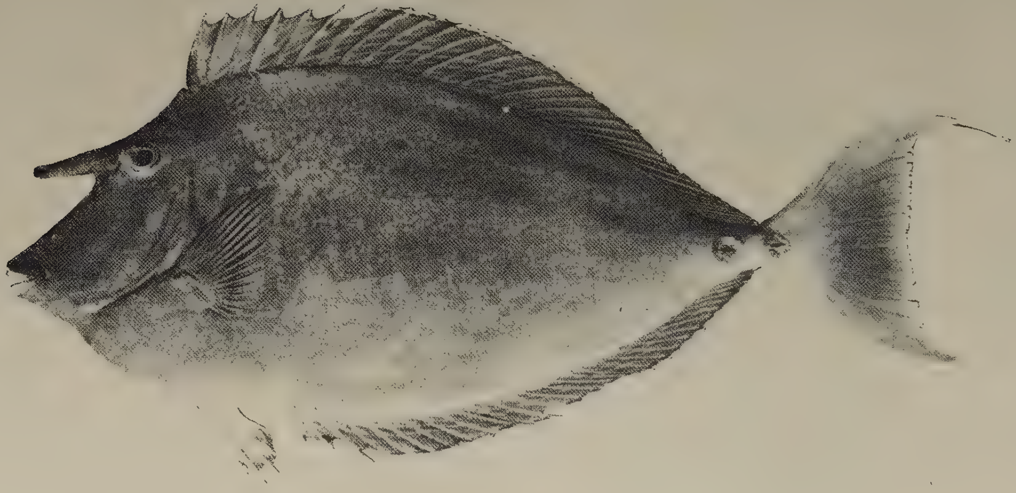

Figure 70.—*Naso unicornis*.

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ACANTHURIDAE — **Naenae**

by Victor A. Honda

Valid name	*Acanthurus olivaceus* (Bloch and Schneider 1801) (Fig. 69)
Synonymy	*Acanthurus nigricans* var. *olivaceus* Bloch and Schneider 1801 *Acanthurus eparei* Lesson 1830 *Acanthurus humeralis* Cuvier and Valenciennes 1835 *Ctenodon erythromelas* Swainson 1839 (error or emendation for *Acanthurus eparei* Lesson) *Harpurus paroticus* Forster 1844 *Acanthurus chrysosoma* Bleeker 1857 (?) *Rhombotides xanthosoma* Bleeker 1865 *Rhombotides olivaceus* Bleeker 1865 *Teuthis olivaceus* Seale 1901 *Hepatus olivaceus* Jordan and Evermann 1905 *Hepatus chrysosoma* Fowler 1928 (from Randall 1956)
Common and vernacular names	Surgeonfish; orange spot tang; naenae

Distribution

Inhabits the main islands. Occurs at Middle Bank, Nihoa, and Necker Island in waters from 33 to 77 m (NMFS survey). Present inshore as far northwest as Maro Reef (Okamoto and Kawamoto 1980). Inhabits deeper waters of the subsurge zone (about 4-128 m), usually over sandy areas interspersed with coral or basalt structures (Jones 1968).

Distinguishing characteristics

D. IX, 23-25; A. III, 22-24; P1. 16-27; Gr. 24-28 (Masuda et al. 1975). Body rather deeply ovoid, greatest depth at middle of pectoral; head deep, compressed, with steep, convex upper profile; jaws slightly produced, lower jaw inferior; mouth small, oblique; teeth broad with sharp cutting edge; margin of opercle oblique, angle below anterior margin of eye; nostrils round, close together, anterior to eye. Last dorsal spine longest; pectoral pointed, equal to head; caudal deep, broad, rays long, pointed; caudal spine depressible in a groove; scales ctenoid, small; lateral line arched following dorsal profile of back (Jordan and Evermann 1905).

In life purplish black, breast bluish, black edged orange bar on shoulder region running posteriorly from upper angle of opercle to area below sixth dorsal spine; dorsal nearly black, membranes slightly bluish; caudal nearly black, same as dorsal, posterior one-third white edged with black; anal same as ventrals edged with black, membranes mottled with blue; pectoral same as ventrals except posterior third dirty-white; iris black, inside edge bright yellow. Orange bar lacking in young specimens but solid orange-yellow in life (Jordan and Evermann 1905; Gosline and Brock 1960).

Life history

The orange-yellow young metamorphose and assume the adult coloration at about 29-55 mm SL (Randall 1956). The species is considered a grazer, picking up large quantities of the substratum while feeding, irrespective of whether the material is rasped away from rock or picked up as loose sand (Jones 1968). As a result, the gut contents include considerable inorganic sediments (Gosline and Brock 1960). Coralline algae, gastropods, and foraminiferans are found in stomachs of fishes in the Marshall Islands, but their presence may be due to accidental ingestion while feeding (Hiatt and Strasburg 1960).

Gear and catch

Naenae is caught mainly in traps although the species is also taken in gill nets. The annual commercial catch in 1976-79 varied from 385 to 963 kg and averaged 556 kg.

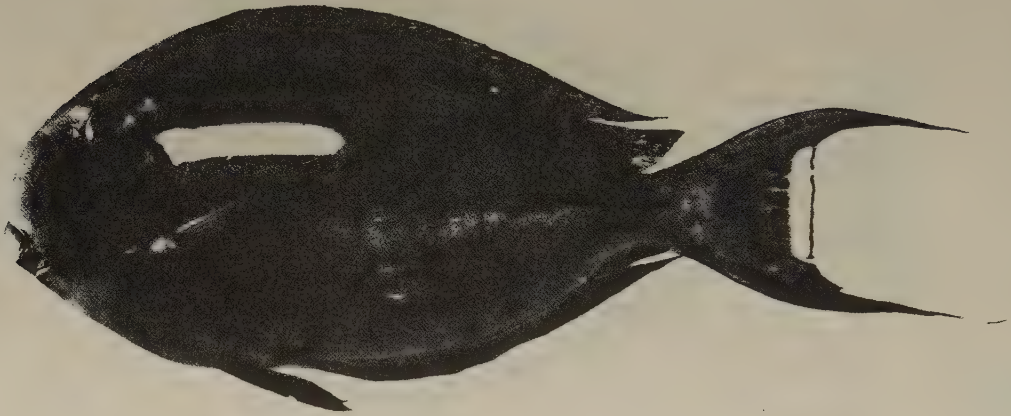

Figure 69.—*Acanthurus olivaceus*.

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by Robert L. Humphreys, Jr.

Valid name	*Seriola dumerili* (Risso 1810) (Fig. 58)
Synonymy	*Caranx dumerili* Risso 1810 *Seriola purpurescens* Temminck and Schlegel 1844 *Seriola dumerili* Weber and De Beaufort 1931 (from Lindberg and Krasyukova 1971)
Common and vernacular names	Greater amberjack; yellowtail; kahala

Distribution

Widely distributed in the NWHI from Middle Bank to Kure Atoll. Usually inhabits the inner reef as well as the outer slopes of the island shelf. Shows considerable vertical mobility ranging from the surface to 247 m.

Distinguishing characteristics

D. I, VII, I, 30-31; A. II, I, 19-21 (Jordan and Evermann 1905; Lindberg and Krasyukova 1971). Body elongated, oval in cross-section. Head conical in profile, eye moderate, mouth large, oblique. Maximum depth at midbody, tapering posteriorly to a short, narrow caudal peduncle. Broad bands of villiform teeth cover jaws, palatines, tongue, and vomer.

Dorsal fin composed of short spinous anterior portion followed by a long, low soft dorsal which is higher anteriorly; anal similar to soft dorsal, preceding spines short. Pectorals short; pelvics inserted posterior to and longer than pectorals; caudal strongly forked (Jordan and Evermann 1905).

Body covered with small cycloid scales; no enlarged scutes along lateral line. Scales not present on opercle, snout, and top of head.

In life predominantly yellow and brown with occasional greenish patches. A thick, prominent yellow stripe extends from maxillary to the eye, then posteriorly from eye, crossing above pectorals to caudal peduncle.

Data from NMFS cruises showed mean lengths and weights of 75.1 cm and 7.24 kg for males and 78.2 cm and 7.79 kg for females. Maximum length was 106.0 cm in males and 149.4 cm in females.

Greater amberjack can be distinguished from its congener, *S. lalandei*, by the presence of 15 or fewer gill rakers on the first lower gill arch, <33 second dorsal rays, maxillary extending back to mideye, and 150-175 transverse scale rows (Gosline and Brock 1960; Lindberg and Krasyukova 1971).

Life history

Based on samples from the Hawaiian Archipelago, size at maturity in females is 54 cm FL (Kikkawa and Everson 1984). Spawning occurs throughout the year with a peak in April. Fecundity estimates range from 1.3 to 4.0 million eggs for fish 83.0 to 118.6 cm FL.

In Hawaii, as elsewhere in the world, the greater amberjack has been implicated in numerous cases of ciguatera.[12] No relationship between size and ciguatoxicity among fish in the Hawaiian Archipelago has been found (Kimura et al. 1982). These findings dispute the commonly held notion in Hawaii of higher probability of ciguatoxin in greater amberjack >9.1 kg. The proportion of toxic fish in the NWHI is similar to that for fish around the main islands.

Ciguatoxin is believed to be transmitted through the food chain and to accumulate more among higher predators such as the greater amberjack. *Decapterus* sp. is the primary component in the diet of the greater amberjack caught in the main islands (Humphreys and Kramer 1984). However, ciguatoxic fish in the size group 4.00-8.99 kg has a lower *Decapterus* and higher bottom-associated prey content than the complementary nonciguatoxic group. These results indicate that a shift toward bottom-associated prey may be responsible for the transmission of ciguatoxin up the food chain.

There are dietary differences between greater amberjack sampled from the NWHI and the main islands. Octopus and bottom-associated prey are the predominant dietary components in the NWHI whereas *Decapterus* and water column-associated prey are predominant in the main islands. In both areas there is a dietary increase of *Decapterus* and water column-associated prey with increasing predator size.

The following growth rate of greater amberjack was determined using a freely fitted von Bertalanffy growth equation of:

$$L_t = 149.3(1-e^{-0.314(t-0.0420)}),$$

where L = fork length (cm) expressed as a function of time t in years (see footnote 10). This equation projects a length of 37.5 cm at 1 year, 67.5 cm at 2 years, and 89.6 cm at 3 years.

A male to female ratio of 60:40 (N = 209) was observed for specimens collected during NMFS cruises in the NWHI. A much larger sample (N = 3,989) from statewide catches shows a ratio of 52:48.[13]

The functional length-weight relationship for 181 greater amberjack ranging from 49.9 to 113.8 cm FL is:

$$W = 2.21 \times 10^{-8} L^{2.9412},$$

where W = weight (kg) and L = fork length (mm) (Uchiyama et al. 1984).

The catch rates of greater amberjack were fairly uniform from Nihoa to Pearl and Hermes Reef; however, the average size of fish caught from Gardner Pinnacles to Pearl and Hermes Reef was larger

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[12] Kubota, W. 1981. Ciguatera fish poisoning cases: A summary from 1900 to December 1980. Pacific Ciguatera Workshop, Honolulu, HI, 18-20 March 1981, WP/7, 14 p.

[13] Polovina, J. J., and B. M. Ito. 1981. Analysis of data from the kahala ciguatera sampling program, April 1979 to December 1980. Pacific Ciguatera Workshop, Honolulu, HI, 18-20 March 1981, WP/1, 4 p

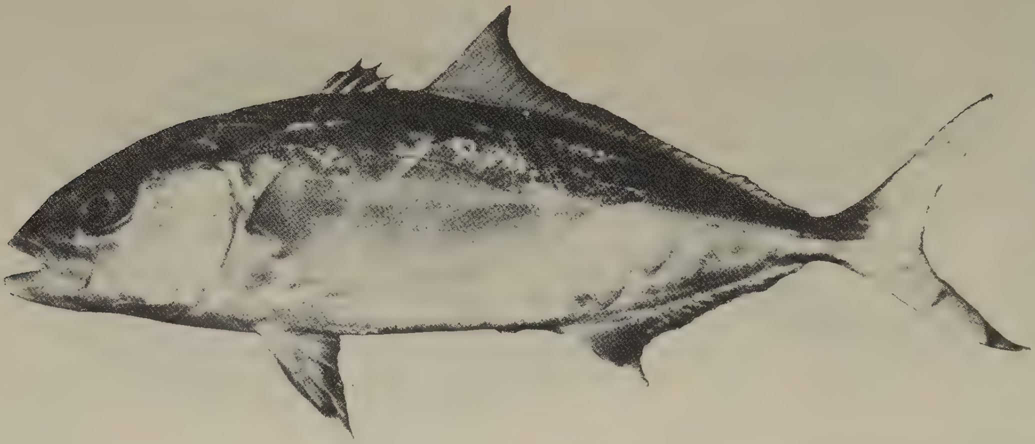

Figure 58.—*Seriola dumerili.*

than that caught from Middle Bank to St. Rogatien (Uchiyama and Tagami 1984). The catch per unit of effort was higher at night (Moffitt 1980).

The vertical mobility of the species theoretically allows it to become associated with members of the snapper-grouper complex; however, competition for bottom-related forage organisms may not be intense or may be limited because it also utilizes *Decapterus* and other water column organisms.

Gear and catch

The greater amberjack is taken mainly by deep-sea handline but also enters traps. Annual landings from the NWHI varied between 614 and 6,311 kg and averaged 3,029 kg during 1959-77.[14] Statewide annual landings for 1961-79 ranged from 13,629 to 47,938 kg and averaged 33,108 kg. Because greater amberjack has been implicated in several ciguatera attacks in Hawaii, the species is generally not sold in the local markets.

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[14] Polovina, J. J., and R. B. Moffitt. 1980. Commercial bottom handline fishing in the Northwestern Hawaiian Islands 1959-77. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-80-11, 2 p.

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LUTJANIDAE — Opakapaka

by Robert L. Humphreys, Jr.

Valid name	*Pristipomoides filamentosus* (Cuvier and Valenciennes 1830) (Fig. 64)
Synonymy	*Serranus filamentosus* Cuvier and Valenciennes 1830 *Chaetopterus microlepis* Bleeker 1869 *Aprion (Aprion) microlepis* Bleeker 1876-77 *Aprion microdon* Steindachner 1876 *Aphareus roseus* Castelnau 1879 *Bowersia violescens* Jordan and Evermann 1904 *Apsilus microdon* Jordan and Evermann 1905 *Aprion filamentosus* Gilchrist and Thompson 1909 *Aprion microlepis* Ogilby 1916 *Aprion roseus* McCulloch 1917 *Pristipomoides filamentosus* Barnard 1927 *Pristipomoides violescens* Jordan and Jordan 1927 *Pristipomoides sieboldii* Fowler 1928 *Pristipomoides microlepis* Fowler 1928 *Pristipomoides microdon* Fowler 1931 *Aprion kanekonis* Tanaka 1935 *Aprion (Pristipomoides) microlepis* Weber and De Beaufort 1936 *Pristipomoides argyrogrammiscus* Smith 1937 *Pristipomoides filamentosus roseus* Abe and Takashima 1956 (from Kami 1973)
Common and vernacular names	Pink snapper; opakapaka

Distribution

Inhabits the outer reef slopes of the islands and banks in the Hawaiian Archipelago. Found in the NWHI from Nihoa to Ladd Seamount on NMFS surveys in depths ranging from 27 to 328 m. Although not caught at NMFS sampling stations at Midway, known to occur there.[18]

Occurs in shallower water in the more northern islands and atolls in the NWHI (based on the maximum capture depth of 328 m at Necker Island, 201 m at Northampton Seamounts, and 108 m at Ladd Seamount). No apparent seasonal variation in distribution (Ralston 1981). Migrates into shallow water at night (based on trap and pot catches during NMFS surveys).

Distinguishing characteristics

D. X, 11; A. III, 8; P1. II, 12, II; P2, I, 5; Gr. 22-26; LLps. 55-65. Body elongate, somewhat laterally compressed. Distinguishable from its three congeners in Hawaii, *P. auricilla*, *P. sieboldii*, and *P. zonatus*, by the V-shape pattern of the vomerine (Gosline and Brock 1960; Kami 1973).

Broad bands of villiform teeth on jaws, palatine, tongue, and vomer. Outer row of teeth in upper and lower jaws canine, increasing in size near the symphysis (Jordan and Evermann 1905; Kami 1973).

Dorsal fin continuous, unnotched, last dorsal ray elongate. Origin of anal fin under base of third or fourth dorsal ray; last anal ray elongate, similar to last dorsal ray. Pelvic fins thoracic, pointed; when extended, tip of pectoral aligns with base of 10th dorsal spine. Caudal bifurcate, lobes usually equal.

Scales ctenoid, moderate. Scales not present on anterior portion of head including jaws, dorsal, and anal fins; small scales present on caudal. Lateral line complete, extending across upper half of body. Seven to eight rows of scales between origin of dorsal fin and lateral line; 14-16 rows between lateral line and origin of anal fin (Jordan and Evermann 1905; Lindberg and Krasyukova 1971; Kami 1973).

In life, rosy, with violet shades, becoming pale ventrally. Dorsal, anal, and caudal fins a combination of red and yellow hues with lavender margins; pelvic fins white (Jordan and Evermann 1905). No evidence of sexual dichromatism apparent from NMFS studies in the NWHI; however, differences occur in pigmentation of large adults collected from Guam (Kami 1973). Anal fin membranes of females clear, those in males dusky with orange and yellow hues at the anterior and posterior extremities.

Size data of opakapaka collected by NMFS reveal a mean length and weight of 53.8 cm FL and 3.06 kg, respectively. Maximum length and weight were 77.9 cm and 8.00 kg, respectively.

Life history

Size and age at maturity are similar between sexes (Ralston 1981). Testicular and ovarian weights increased greatly in fish from 30-35 cm to 35-40 cm. The age at maturity in both sexes is approximately 2 to 3 years (Ralston 1981; Uchiyama and Tagami 1984). A preliminary gonadal study showed heterogeneous egg development within the ovaries (Kikkawa 1980). A comparison of monthly mean gonadal-somatic indices revealed a single spawning period each year from June through December; spawning peaks in August (Kikkawa

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[18] Ralston, S., Fishery Biologist, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, pers. commun. 1983.

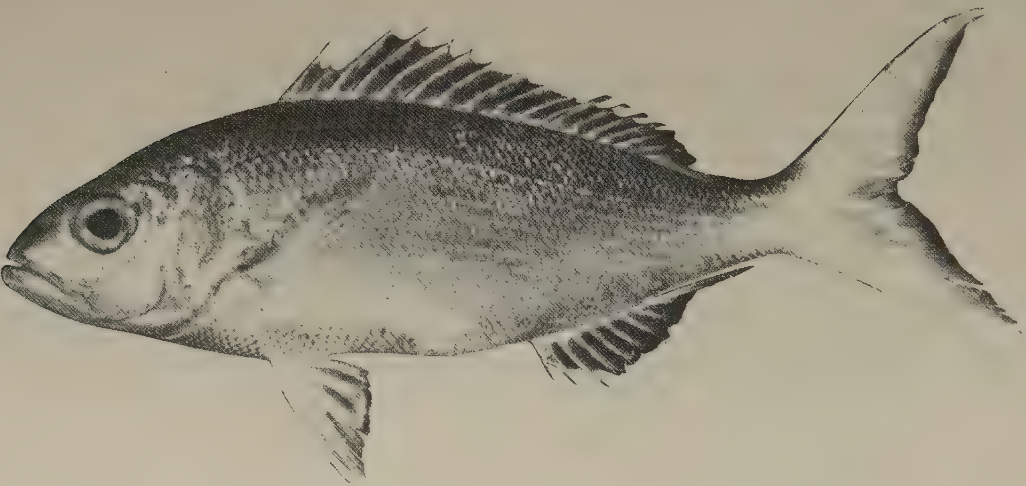

Figure 64.—*Pristipomoides filamentosus.*

1984). Fecundity estimates ranged from 478,000 to 1,461,875 eggs for fish ranging from 48.7 to 76.3 cm FL.

A preliminary analysis of spews from opakapaka in the NWHI shows *Pyrosoma* sp. as the dominant prey. Other items include fish, crustaceans, and molluscs (see footnote 18). *Pyrosoma* is also the predominant prey item of opakapaka caught at Guam (Kami 1973).

Currently there is disagreement on age and growth of opakapaka. Using annuli on the sagitta to estimate the age of opakapaka, NMFS studies indicate a von Bertalanffy growth equation as follows:

$$L_t = 97.1(1-e^{-0.31(t-0.02)}),$$

where L_t = fork length (cm) expressed as a function of t in years (see footnote 10). The projected length-age relationships are: 25.4 cm at 1 year, 44.5 cm at 2 years, 58.6 cm at 3 years, 68.8 cm at 4 years, and 76.4 cm at 5 years. Age estimates derived from whole counts of daily increments on sagittae agree well with those obtained from annuli counts.

Using increment widths as a measure of growth rate, Ralston and Miyamoto (1983) derived the following von Bertalanffy growth curve:

$$L_t = 78.0\ (1-e^{-0.146(t+1.67)}).$$

The projected length-age relationships are 25.2 cm at 1 year, 32.4 cm at 2 years, 38.6 cm at 3 years, 43.9 cm at 4 years, and 48.5 cm at 5 years. There is no significant difference in growth rate between sexes and for fish around the main islands and NWHI (Ralston 1981).

Among 452 opakapaka examined from Hawaii, the sex ratio was 50:50 (Ralston 1981). However, there is a greater number of male than female specimens collected from Guam (Kami 1973).

A functional length-weight relationship derived from 471 specimens ranging from 23.4 to 77.9 cm is:

$$W = 3.58 \times 10^{-8}\ L^{2.8806},$$

where W = weight (kg) and L = fork length (mm) (Uchiyama et al. 1984). The equation indicates that growth is allometric.

Studies on spatial homogeneity within the species habitat range provide some evidence of size-specific abundance differences with depth (Ralston 1981). Results from French Frigate Shoals and Necker Island show similar patterns of juvenile confinement to narrower depth ranges than adults. Maro Reef juveniles and adults, however, appear to occupy the same range of depths.

Catch per unit effort data indicate a higher relative abundance at Necker Island, French Frigate Shoals, and Brooks Banks than elsewhere in the NWHI (Uchiyama and Tagami 1984). Opakapaka is the dominant bottom fish species at Necker Island (44.6%), French Frigate Shoals (52.5%), and Brooks Banks (40.0%). A similar trend was noted by Moffitt (1980).

Preliminary results from electrophoretic analysis of 50 loci from opakapaka sampled throughout the Hawaiian Archipelago indicate low genetic variability; however, the results imply, but do not prove, a single stock within Hawaii because of the small sample size (Shaklee and Samollow 1980).

Gear and catch

Opakapaka is caught with deep-sea handline. Annual reported landings from the NWHI ranged between 349 and 12,828 kg and averaged 4,587 kg during 1959-77 (see footnote 14). Annual statewide landings in 1961-79 varied from 23,964 to 93,148 kg and averaged 52,683 kg. Commercially the most important bottom fish in Hawaii, opakapaka has dominated the statewide landings of bottom fish since 1948.

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Review and Current Status of Research on the Biology and Ecology of the Genus *Pseudopentaceros*

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ABSTRACT

The genus *Pseudopentaceros* has two species, the pelagic armorhead, *P. wheeleri*, confined to the North Pacific, and *P. richardsoni*, confined to the Southern Hemisphere. Center of abundance and spawning grounds for pelagic armorhead is the southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts and for *P. richardsoni* the Walvis Ridge. Adult pelagic armorhead typically inhabit the summits and upper slopes of the SE-NHR seamounts and open ocean adults and juveniles occur in waters of the northern and northeastern Pacific.

Pelagic armorhead on the SE-NHR summits aggregate at night and typically remain dispersed during daylight hours. Surface and near surface aggregations have been reported from the northern and northeastern Pacific. Within the SE-NHR, diet consists mainly of mesopelagic organisms associated with the deep scattering layer. The peak spawning period within this region extends from late December through January. Among pelagic armorhead collected from the Hancock Seamounts (located within the SE-NHR), females were significantly larger than males. Results of various age and growth studies on pelagic armorhead indicate either 2-3 years or 7-9 years for the age composition at the SE-NHR seamounts.

Morphological variation of pelagic armorhead has led to taxonomic difficulties. Three body types—lean, intermediate, and fat—occur among SE-NHR pelagic armorhead. The lean and intermediate types were described as *P. wheeleri* and the fat type as *P. pectoralis*. Preliminary results of a morphological investigation demonstrate intergradation of characters between fat and intermediate and intermediate and lean. These results cast doubt on the existence of two separate species in the North Pacific. A hypothetical life history, which assumes the existence of only one North Pacific species is presented; we suggest that fat types undergo a morphological change to intermediate and lean types after settlement on the seamounts.

INTRODUCTION

A recent revision of the Family Pentacerotidae by Hardy (1983) placed the pelagic armorhead[1] into the genus *Pseudopentaceros* and recognized three separate species. Previously, only a single species, *Pentaceros richardsoni*, was recognized. Hardy's revision includes a single species, *Pseudopentaceros richardsoni*, in the Southern Hemisphere and two species, *P. wheeleri* and *P. pectoralis*, in the North Pacific. *Pseudopentaceros richardsoni* differs from *P. wheeleri* and *P. pectoralis* in meristic characters (26 total vertebrae and ⩾32 midline throat scales from isthmus to pelvic fin insertions) and morphometric characters (least bony interorbital width ⩾3.0 in head length and body depth at first anal spine >3.0 in standard length) distinguish *P. wheeleri* from *P. pectoralis*. Since virtually all of the biological information on pelagic armorhead predates Hardy's revision, however, considerable uncertainty exists concerning the identity of the species in past literature. Hereafter, we refer to *P. wheeleri* and *P. pectoralis* as "pelagic armorhead" unless species identification is discernible from a reference. All *Pseudopentaceros* recorded from southern latitudes will be referred to as *P. richardsoni* since its distribution is known only from the Southern Hemisphere and the other two species are unrecorded from this region.

The Soviet discovery in 1967 of vast concentrations of pelagic armorhead near the seamounts of the southern Emperor-northern Hawaiian Ridge (SE-NHR) and later discovery of concentrations of *P. richardsoni* from seamounts of the Walvis Ridge focused attention on a genus previously considered rare and whose biology and ecology were virtually unknown. Subsequently, biological investigations (primarily on pelagic armorhead) were initiated by Soviet and Japanese researchers. Although these studies have contributed much new information, our current understanding of various life history aspects of *Pseudopentaceros* remains incomplete.

A compilation of the current biological and ecological information on *Pseudopentaceros* will initially be presented in this review. Subsequently, we will focus on preliminary results from our study of morphological variation in pelagic armorhead and suggest a hypothetical life history.

LIFE HISTORY INFORMATION

Distribution

The distribution of *Pseudopentaceros* appears in Figure 1. Hardy (1983) reports the general distribution of *P. wheeleri* from Japan to Hawaii in the northern Pacific Ocean. Collection sites of specimens examined were Kimmei (actually Koko) Seamount in the southern Emperor Seamount Chain, from Hancock Seamounts in the northern Hawaiian Ridge, and off Hachijo Island, Japan. Hardy reported the distribution of *P. pectoralis* extending from Hawaii to the northern and northeastern Pacific across to the west coast of North America and south to California. The distribution of the two species overlap in the central North Pacific. Collection sites of *P. pectoralis* material examined by Hardy (1983) include Ladd Seamount in the northern Hawaiian Ridge, oceanic waters of the northern Pacific Ocean, and off the coasts of Oregon and California. Morphological information in Sasaki (1974), Takahashi and Sasaki (1977), and from our observations supports this distribution.

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[1] Pelagic armorhead was proposed as a common name for *Pentaceros richardsoni* y Follett and Dempster (1963); it is not meant to indicate habitat preference

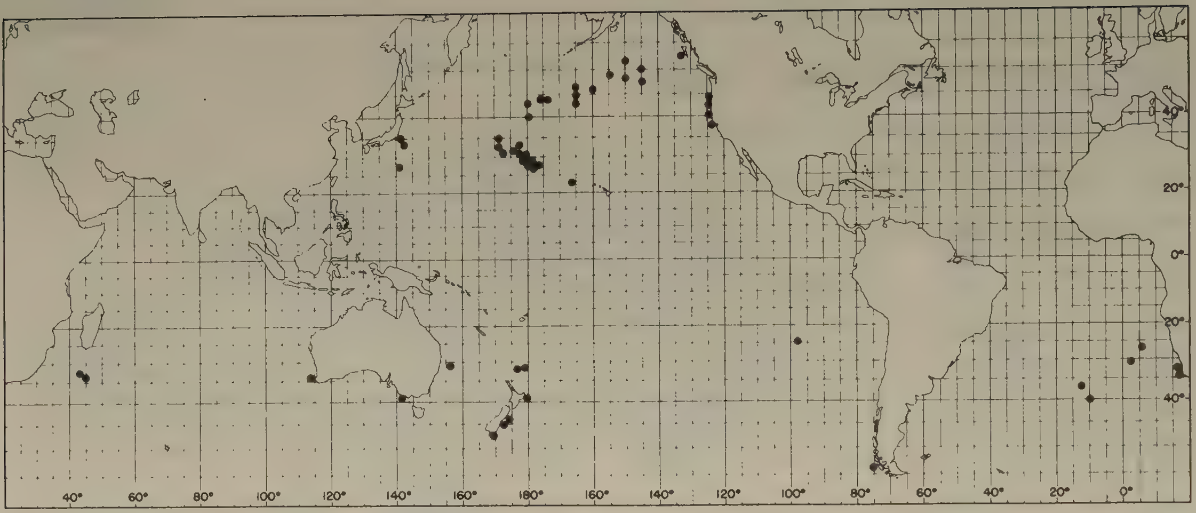

Figure 1.—Worldwide distribution of *Pseudopentaceros*. Solid dots in the Southern Hemisphere represent *P. richardsoni* and in the North Pacific Ocean, *P. wheeleri* and *P. pectoralis* combined.

Previous to Hardy's revision, captures of pelagic armorhead were from California (Follett and Dempster 1963; Smith 1965), Oregon (Wagner and Bond 1961), British Columbia (Clemens and Wilby 1961; Hart 1973), around Japan near the Boso Peninsula (Abe 1957), off Hachijo Island (Abe 1969), the Ogasawara Islands (Zama et al. 1977), in northern oceanic waters south of the Aleutian Islands and around the Gulf of Alaska (Welander et al. 1957; Larkins 1964; Honma and Mizusawa 1969; Chikuni 1970; Hokkaido University, Faculty of Fisheries 1976, 1979, 1981, 1982, 1983; Randall 1980). Among the central North Pacific seamounts, pelagic armorhead have been reported from Mellish Bank (Takahashi and Sasaki 1977), from Koko, Yuryaku, and Kammu of the southern Emperor Seamount Chain and from Colahan, C-H, Northwest (NW) and Southeast (SE) Hancock, unnamed Seamounts 10 and 11 (Sakiura 1972) and from Kure Atoll and Ladd Seamount (Randall 1980), all located along the northern Hawaiian Ridge. Two specimens have been captured in the central region of the Hawaiian Ridge at Laysan Island and French Frigate Shoals (Tagami, manuscr. in prep.). Surveys conducted elsewhere in the North Pacific have generally not found pelagic armorhead. From distribution records of pelagic armorhead and known oceanographic conditions in the northeast Pacific and SE-NHR seamounts, Chikuni (1971) proposed that pelagic armorhead are capable of inhabiting waters of 5°-20°C (8°-15°C optimum). The SE-NHR seamounts include Koko, Yuryaku, Kammu, Colahan, C-H, NW and SE Hancock, and unnamed Seamounts 10 and 11.

Borets (1980) reported that pelagic armorhead "fry" from 8 to 40 mm long were collected in ring trawl tows conducted near the SE-NHR seamounts. Highest catches of these transformed juveniles were made near the Milwaukee Seamounts (Yuryaku and Kammu) but these juveniles were not found near Koko Seamount. Numerous hauls for young pelagic armorhead conducted near the northern Hawaiian Ridge during winter collected only a small number of eggs and larvae. No reports were found on the capture of eggs and larvae of pelagic armorhead outside of the SE-NHR region. The existence of eddies and meandering surface circulation over the SE-NHR and their intensification during the winter is thought to retain early life stages of pelagic armorhead in the seamounts region (Borets 1980).

Pseudopentaceros richardsoni in the South Pacific is known from Derwent Hunter Seamount (Sasaki 1978), off New Zealand and the south coast of Australia (Hardy 1983), and the Sala y Gomez Ridge (Borets 1980). In the South Atlantic, *P. richardsoni* is known from Cape Point, South Africa (Smith 1964), from Valdivia Seamount and other seamounts along the Walvis Ridge (Pakhorukov 1980; Sasaki 1986), in the South Indian Ocean from the Madagascar Ridge (Kotlyar 1982), and off western Australia (Hardy 1983). Juvenile *P. richardsoni* have been collected from the South Pacific off Cape Horn (Smith 1964), off Kermadec Island and over the South Fiji Basin (Hardy 1983), and in the South Atlantic from near Gough Island and Tristan da Cunha (Penrith 1967; Borets 1980; Pakhorukov 1980). No reports were found on the distribution of earlier life stages of *P. richardsoni*. The center of abundance for *P. richardsoni* is the seamounts of the Walvis Ridge.

Data for 1969-81 show that virtually all of the pelagic armorhead caught in the trawl fishery at the SE-NHR seamounts ranged from 26 to 33 cm fork length (FL) in an overall size range of 15-40 cm FL (Takahashi and Sasaki 1977; Sasaki 1982). The mean annual length has increased somewhat from a low of 27.4 cm in 1972 to 32.1 cm FL in 1981 (Table 1). Takahashi and Sasaki (1977) and

Table 1.—Length data of pelagic armorhead taken by Japanese trawlers, all seamounts combined (Takahashi and Sasaki 1977; Sasaki 1982).

Year	Sample size	Mean fork length (cm)	Range of fork lengths (cm)
1969	375	29.2	24-36
1970	166	29.2	26-34
1971	4,400	28.9	24-40
1972	6,410	27.4	20-34
1973	3,138	29.0	25-35
1974	20,724	28.8	21-37
1975	11,736	28.9	23-35
1976	8,517	29.5	15-35
1978	5,508	31.3	23-44
1979	2,412	30.9	21-39
1981	2,664	32.1	27-40

Borets (1980) report little variation in size composition among the seamounts of the SE-NHR. Takahashi and Sasaki (1977) reported the tendency of the largest pelagic armorhead to occur in the trawl catches at 300-390 m depths and smaller fish at 200-290 and 400-490 m. Size distribution data for pelagic armorhead from other areas are scant; fish from these areas generally fall within the size range noted above. The largest recorded size for pelagic armorhead is a 54.7 cm FL specimen from French Frigate Shoals (Tagami, manuscr. in prep.). Analysis of sex-length data on pelagic armorhead taken from the Hancock Seamounts during 1978-82 indicated that the greater mean fork length of females and the annual pattern of this difference were highly significant (see Table 2). *Pseudopentaceros richardsoni* taken in the trawl fishery on the Walvis Ridge (Pakhorukov 1980) ranged from 35 to 48 cm long (mean length, 41 cm). The largest recorded *P. richardsoni* is a 55.5 cm total length (TL) specimen from South Africa (Smith 1964).

Adult and juvenile *P. pectoralis* have been collected from surface and near surface waters in the open ocean (Sasaki 1974), and in the SE-NHR, adult pelagic armorhead occur over summit depths of 160 to 400 m and to acoustically recorded depths of 800 m (Borets 1980). Eggs, larvae, and small juveniles of pelagic armorhead appear restricted to the surface layer (Borets 1975, 1979; Fedosova and Komrakov 1975). Adult and juvenile *P. richardsoni* have been collected from the surface; adults have also been collected at 1,000 m (Kotlyar 1982; Hardy 1983).

Table 2.—The ANOVA of length data, by sex, for pelagic armorhead taken at Hancock Seamounts by Japanese trawlers (NS = P > 0.05; *** P ⩽ 0.001).

Year	Number of males	Mean fork length of males (cm)	Number of females	Mean fork length of females (cm)	ANOVA		
					Source	df	PR>F
1978	222	29.1	325	29.7	Sex	1	***
1979	461	29.0	577	29.7	Year	4	***
1980	2,302	29.7	1,759	30.5	Sex and year	4	NS
1981	620	29.7	817	30.7			
1982	578	29.9	790	30.7			

Behavior

Reports from Japanese whaling ships working the northeast Pacific during the summer months of 1967-69 noted the handline capture of numerous pelagic armorhead at night under the ships' lights. Pelagic armorhead were also found in the stomachs of sei whales; the whales appeared satiated in the early morning and near evening. Chikuni (1970) concluded that pelagic armorhead in this area are capable of forming large near-surface aggregations during daylight and night hours. Aggregations of pelagic armorhead are also present over the summits of the SE-NHR seamounts at night but are typically absent during the day. Early Soviet surveys over these summits acoustically detected aggregations ranging in average thickness from 15 to 35 m (Sakiura 1972). Variation in nocturnal catches reported by Nasu and Sasaki (1973) suggests these aggregations exhibit a patchy distribution over the summits.

Sakiura (1972) reported that acoustically detected nocturnal aggregations of pelagic armorhead near the summits ascended to the level of the thermocline and dispersed after dawn. This position was maintained throughout the day until dusk when schools began descending over the summits. Kitani and Iguchi (1974) proposed that this nocturnal descent actually extends to a depth below the summit level whereas Sasaki (1974) reported that vertical movements were ambiguous over some of the seamounts but clearly evident at SE Hancock Seamount. An alternate explanation is that pelagic armorhead inhabit the slope areas during daylight and ascend to the summit upon nightfall. These observations and interpretations based on acoustical observations may be misleading, however, due to the movements of high densities of micronekton over some seamounts (Boehlert and Seki 1984). Further studies are needed to clarify the periodicity, predictability, and range of these movements.

Feeding habits

Borets (1975) reported that the feeding period of SE-NHR pelagic armorhead extends from March to September. During this period, 40% of the stomachs examined were empty while another 40% had only remnants of food; full stomachs were rarely encountered. Borets also noted that during the feeding period, the condition factor of fish was higher compared with fish during the winter.

Sakiura (1972) reported that during a 24-h period, pelagic armorhead of the SE-NHR feed during daylight, and that feeding peaked from 0800 to 1000. Field observations by T. K. Kazama and W. B. Barnett (both of Southwest Fish. Cent. Honolulu Lab.) on the condition and volume of stomach contents indicated feeding occurred during daylight, primarily in the morning and late afternoon. However, Kitani and Iguchi (1974) found a higher proportion of stomachs with food during 0000-0800. Fedosova and Komrakov (1975) reported that over a 24-h period, juvenile pelagic armorhead (8.5-23.0 mm long) collected within the SE-NHR region showed evidence of round-the-clock feeding which peaked in the morning and evening hours. No data on time of feeding and feeding periods of *P. richardsoni* are available.

The important prey items in the diet of SE-NHR pelagic armorhead, as reported in Sakiura (1972), were surface dwelling crustaceans. However, information on the feeding habits of these fish in Nasu and Sasaki (1973), Japan Fisheries Agency (1974), Sasaki (1974), Borets (1979), and Kazama and Barnett (field observations) indicates that a major portion of the diet consists of deep-scattering-layer (DSL) organisms. Specifically, these include amphipods, copepods, euphausiids, macrura, pteropods, sergestids, tunicates, myctophids, and mesopelagic fishes. Borets (1975) reported that 73 species of zooplankton (mainly copepods and amphipods) have been identified from stomachs of SE-NHR pelagic armorhead, including six species of Radiolaria.

Feeding periodicity data suggest that pelagic armorhead preferentially feed on that portion of the DSL whose vertical descent is blocked by the expanse of the seamount summit. Although this explanation accounts for the presence of pelagic armorhead aggregations near the summits around dawn, it does not explain their presence over the summits in the evening when stomachs are typically empty. Fedosova (1980) linked times of favorable feeding conditions for young pelagic armorhead to increases in the winter-spring plankton biomass during warm years. Fedosova and Komrakov (1975) reported that the major prey items of 8.5-23.0 mm long pelagic armorhead from the SE-NHR were copepods, chaetognaths, and larval bivalve mollusks. Copepods had the highest frequency of occurrence (93.8%); the dominant species was *Clausocalanus arcuicornis* followed by *Oithona similis* and *Mecynocera clausi*. Size of food items ranged from 0.35 to 9.0 mm. No reports on the feeding habits of *P. richardsoni* are available.

Reproduction

Information on the spawning period of pelagic armorhead is available only for the SE-NHR seamounts; reproductive adults have not been recorded from oceanic waters of the northern and northeastern Pacific. Bilim et al. (1978) reported prespawning conditions in mid-November; the spawning period began in early December and peaked during late December through January. In February, spawning had largely been completed and by March all mature females were spent. Chen (1980) reported that some individuals at Kammu Seamount had well-developed gonads during May. Borets (1975) commented on the absence during the spawning period of nearly ripe and running ripe females from bottom trawl catches over the SE-NHR seamounts and suggested that pelagic armorhead spawn in midwater. Reproductive adults of *P. richardsoni* have been reported from the Walvis Ridge (Borets 1980), but no information was available on time of spawning.

A histological study of oocyte development in pelagic armorhead from the SE-NHR seamounts was conducted by Bilim et al. (1978). Results indicated that during the spawning season, only one group of oocytes undergo synchronous development up to the time of hydration. The hydration process and release of eggs are asynchronous. During spawning, eggs are released in four to six batches and average 20,000 per batch. Borets (1979) reported that fecundity estimates of 30 cm long females from three SE-NHR seamounts ranged from 99,000 to 110,000 eggs. No information was available on fecundity of *P. richardsoni*.

Age and growth

An analysis of scales from two specimens of pelagic armorhead, 22 and 32 cm FL, indicated that these fish were 3 and 6 years old, respectively (Chikuni 1970). From these results and data indicating that trawl caught pelagic armorhead from the SE-NHR seamounts averaged 30 cm FL, Chikuni surmised that such fish were 5-7 years old. Results of an age and growth study reported in Borets (1979) indicate that a 30 cm FL fish is 7-9 years old. The data also indicate that growth rate of pelagic armorhead at various seamounts within the SE-NHR is similar up until an age of 5-6 years and the majority of the trawl catch is composed of 6-8 year olds. Preliminary results from an analysis of growth increments on the sagitta, however, indicate an age of 2-3 years for a 30 cm FL individual and a large proportion of 2-year olds in the SE-NHR trawl catches (J. H. Uchiyama and J. D. Sampaga, Southwest Fish. Cent. Honolulu Lab., pers. commun. March 1985). Hart (1973) reported that a specimen held in captivity at Vancouver Aquarium for 3 years grew from 25.4 to 32.9 cm. According to the data presented in Borets (1979), such a growth increase in the wild from a similar initial size would require 4-5 years.

Parasitism

Kazatchenko and Kurochkin (1974) reported that the copepod *Pennella hawaiiensis* infested 59% of pelagic armorhead (range 44-80%) examined from trawl catches in the SE-NHR seamounts. Kurochkin (1985) stated that the early marketing of Soviet catches of pelagic armorhead (some 133,000 tons) was temporarily prohibited until the origin of the dark formations in the musculature were attributed to this parasite and found nonhazardous for human consumption. The frequent presence of another ectoparasite was noted among pelagic armorhead at SE Hancock Seamount (Japan Fisheries Agency 1974); we have rarely seen this unidentified parasite which resembles a cooked grain of rice. A preliminary survey of the parasitofauna of *P. wheeleri* and *P. pectoralis* taken from the Hancock Seamounts revealed the presence of monogenetic and diagenetic trematodes, larval nematodes, and crustaceans; all are currently being identified. All four types of parasites were present in a sample of 20 *P. wheeleri* whereas only the monogenetic trematodes and larval nematodes occurred in eight *P. pectoralis*. Larval nematodes were the only parasites present in three *P. pectoralis* which were collected from oceanic waters of the northeastern Pacific. The only record of parasites in *P. richardsoni* is that of larval cestodes (*Gymnorhynchus gigas*) found in the musculature of specimens collected from the Whale (Walvis) Ridge (Alioshkina et al. 1985).

MORPHOLOGICAL VARIATION

Description and available biological data

Before Hardy's recognition of two species of *Pseudopentaceros* in the North Pacific, the existence of morphological variation in pelagic armorhead and its characterization into two to three body types was reported in Kuroiwa (1973), Japan Fisheries Agency (1974), Sasaki (1974), Takahashi and Sasaki (1977), Zama et al. (1977), and Chen (1980). These types were subjectively classified by body depth and appearance as the fat, lean, and intermediate types (Fig. 2).

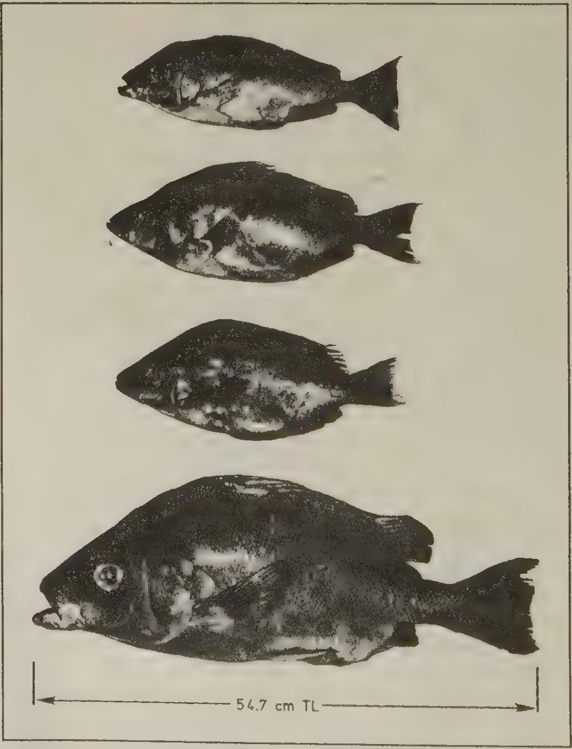

Figure 2.—Specimens representing the various body types of pelagic armorhead. Types starting from the top: lean, intermediate, fat, and a large adult.

The fat type is deeper bodied and that portion of the body below the dorsal fin appears somewhat "square-shaped" in profile. Body coloration is dark blue dorsally and whitish ventrally; dorsal spots occur on some individuals. Juvenile pelagic armorhead resemble the fat type in body profile and according to Honma and Mizusawa (1969), the coloration is basically blue dorsally and white ventrally. Coloration along the dorsal and lateral regions is highly mottled. Small juveniles (8-15 mm FL) collected by the National Marine Fisheries Service (NMFS), Honolulu Laboratory (HL) personnel from surface waters above the Hancock Seamounts resemble the juvenile fat type in body profile and coloration. Adult and juvenile fat type collected from oceanic waters of the northern and northeastern Pacific and examined by the senior author are invariably *P. pectoralis*. Some of the adult fat type taken from the SE-NHR seamounts, however, are less vivid in coloration and have standard length/body depth at first anal spine (SL/BDFAS) ratios which are intermediate between *P. pectoralis* and *P. wheeleri*. Identity of the small juveniles from the Hancock Seamounts has not been determined.

The lean type is characterized by a relatively shallow body, particularly in the posterior portion. Body coloration is uniformly light brown, and spots are absent. We have seen some very emaciated lean individuals at the Hancock Seamounts as have Takahashi and Sasaki (1977). These fish possess an even shallower body with skin which is easily ruptured and exhibit a discoloration of the viscera, suggesting a poor physiological condition. The intermediate type has a body depth in between the other two types but the coloration coincides with the lean type. Large deposits of fat are commonly found in the visceral cavity of the intermediate and fat types whereas these fat deposits are usually reduced in the lean type and absent among very lean individuals. The intermediates and leans are the predominant morphotypes found at the SE-NHR seamounts and have not been recorded from oceanic waters of the northern and northeastern Pacific. Preadult stages of intermediates and leans have not been reported. Numerous lean and intermediate types examined by the senior author (taken from the SE-NHR seamounts) were virtually all identified to *P. wheeleri*.

Trawl specimens collected at the Hancock Seamounts during research cruises of the NMFS, HL yielded approximate male to female ratios as follows: 2:1, 1:2, and 1:1 for the lean, intermediate, and fat type, respectively. In commercial catches, however, a ratio of 1.2:1 occurs in the SE-NHR seamounts (Nasu and Sasaki 1973; Japan Fisheries Agency 1974).

Four large adult specimens >42 cm FL have been collected outside of the SE-NHR seamounts along the Hawaiian Ridge. One of the specimens served as the holotype for *P. pectoralis* in Hardy's revision of *Pseudopentaceros* and two identified to *P. wheeleri*. The fourth specimen had a head length-least interorbital width (HL/LIW) ratio of *P. wheeleri* and a SL/BDFAS ratio of *P. pectoralis*. Thus these large specimens show variation as do smaller fish (Fig. 2).

Before the publication of Hardy's revision, a morphometric and meristic study was initiated to elucidate the nature and significance of the body type variation in pelagic armorhead. A total of 342 specimens were examined; the sample consisted of 86 lean, 110 intermediate, and 146 fat types collected from NW and SE Hancock Seamounts. Each specimen was examined for 12 meristic and 11 morphometric characters. Results of an analysis of variance (ANOVA) on the meristic characters show no significant differences between means compared by body type, sex, and seamount. No meristic differences were presented in Hardy (1983) to distinguish between *P. wheeleri* and *P. pectoralis*. The ANOVA results on the morphometric characters showed highly significant differences within sex and body type for each morphometric character. To ascertain whether these differences could be used in distinguishing between body types, morphometric values were converted into ratios relative to SL (SL/body measurement). Results with SL/greatest orbit length, SL/least interorbital width, and SL/snout length show that ratio values overlap all body types for each of these body proportions (Fig. 3). All three body types show a range of ratio values which overlap in SL/head length and SL/predorsal length (Fig. 4). No such overlap occurred between fats and leans in SL/predorsal to prepelvic length and SL/maximum body depth although each of these types overlapped with the intermediate range. One of two characters presented by Hardy (1983) to distinguish *P. wheeleri* from *P. pectoralis* and examined in this study was HL/LIW. The ranges of both HL/LIW values in each type show a large overlap (Fig. 5). Furthermore, the range of HL/LIW values for each body type includes the ratios 2.9 and 3.0, which represent the maximum HL/LIW value for *P. pectoralis* and minimum HL/LIW value for *P. wheeleri*, respectively (Hardy 1983). Although the above results are from a preliminary study, results of a more comprehensive morphometric and electrophoretic examination of body types will be forthcoming (R. L. Humphreys and G. Winans, Southwest Fish. Center Honolulu Lab., report in prep.).

In Hardy's study, the type material for *P. wheeleri* included 12 specimens from 23.7 to 30.2 cm SL, and for *P. pectoralis*, 9 specimens from 6.6 to 42.5 cm SL. Only four specimens of *P. pectoralis*, however, were of similar size to the *P. wheeleri* material; the rest of the *P. pectoralis* were juveniles and a large adult specimen. Furthermore, it appears that no fat type specimens from the SE-NHR seamounts were available to Hardy. At this point, the existence of two separate species within the North Pacific seems doubtful. No information is available which would dispute the validity of *P. richardsoni* as a separate species constituting all pelagic armorhead in the Southern Hemisphere (Fujii 1986).

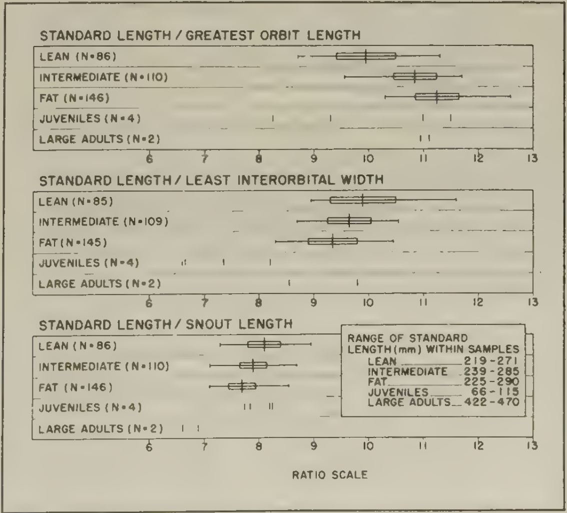

Figure 3.—Ratios of various morphological characters separated by body type, juvenile, and large adult stages. For body type, arithmetic mean is indicated by vertical lines, ±1 standard deviation (boxes), and range (horizontal lines). For juveniles and large adults, vertical lines indicate actual values.

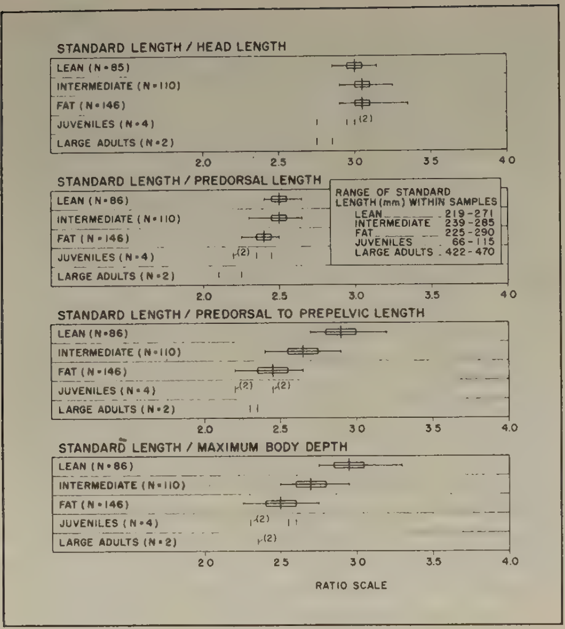

Figure 4.—Ratios of various morphological characters separated by body type, juvenile, and large adult stages. For body type, arithmetic mean is indicated by vertical lines, ±1 standard deviation (boxes), and range (horizontal lines). For juveniles and large adults, vertical lines indicate actual values.

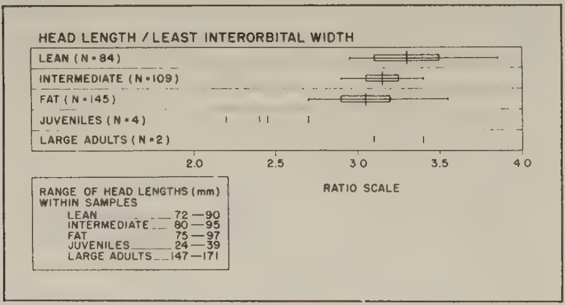

Figure 5.—Ratios of least interorbital width into head length, separated by body type, juvenile and large adult stages. For body type, arithmetic mean is indicated by vertical lines, ±1 standard deviation (boxes), and range (horizontal lines). For juveniles and large adults, vertical lines indicate actual values.

A hypothetical life history of pelagic armorhead

Life histories of pelagic armorhead have been proposed by Chikuni (1970) and Borets (1979, 1980). Chikuni suggested that larvae are dispersed by surface currents away from the seamounts into an area bounded by lat. 15° and 55°N. Early development was thought to be pelagic in surface or midlayer waters with a shift to a demersal existence over seamounts when the fish are 4-5 years old. Borets reported that pelagic armorhead remain pelagic up to age 7 whereupon a change to a demersal habitat occurs and the fish form aggregations over seamounts. Furthermore, the new array of environmental conditions encountered by this habitat change affects the growth and metabolic activity of the fish. Once settled, the fish do not leave the proximity of a given seamount.

The following life history we propose is based, in part, on these previous life history proposals and represents an attempt at incorporating data on morphological variation and current biological and ecological information into a general description of the life history of pelagic armorhead. The crucial assumption in this life history is that there is only one species of pelagic armorhead. The center of reproduction is the SE-NHR seamounts. In the early planktonic stage, they are initially contained by surface currents over the SE-NHR seamounts; individuals rapidly develop into a nektonic stage and actively move away from the seamounts before reaching 5 cm FL. The juveniles are epipelagic and are confined to a temperature regime of 5°-15°C. All juveniles are actually young fat types; juveniles resembling the lean or intermediate types do not exist. The juvenile and adult fat type represent the prereproductive, dispersal phase of the life history; during this phase, energy is stored through an accumulation of body fat. The majority of the fat type change to a demersal existence over the seamounts upon reaching 26-33 cm FL. This shift in habitat involves a change of body coloration, reproductive development, and a gradual loss in body depth and fat content. All fat type fish undergo a transition to the intermediate type upon settlement over the seamounts. The lean type represents a further transition from the intermediate type. The factors which determine the time of transition from the fat type to the intermediate and lean type are probably time of year relative to the reproductive season, size at settlement, and availability of food during settlement. The very lean type represents individuals which have previously spawned and had originally settled at a less than optimum size; the energy demands incurred eventually depleted these fish of virtually all energy reserves. These fish are subsquently susceptible to high mortality. It should be emphasized, however, that upon settlement, the onset of reproductive activity may be energetically the most costly physiological process. The very lean type represents the minimum fork length of settled individuals at the seamounts and would explain the apparently smaller fork lengths among these fish and why pelagic armorhead <26 cm FL are rarely found in trawl catches. On the other hand, an upper limit of about 33 cm FL occurs among the majority of transitional individuals at the seamounts. This phenomenon is attributed to a drastic reduction in growth upon settlement; hence, increases in length and weight are largely confined to the open ocean fat type. The infrequently captured large adults which resemble the fat and intermediate types represent ''strays'' which undergo a protracted fat type phase and eventually undergo settlement at a much larger size compared to the rest of the population. Additionally, a drastic reduction in growth and the onset of reproductive activity would also occur in these individuals upon settlement.

We also propose that recruitment of fat type to the SE-NHR seamounts is probably continuous but at a low level. This pattern of recruitment, coupled with a rapid transition to the intermediate phase, would explain the low percentage of fat types in trawl catches from this region. No theory is advanced to explain the mechanism responsible for the return of open ocean fat type to the seamounts. Finally, if all pelagic armorhead undergo an initial fat type phase, this would imply the existence of a pelagic population removed from the seamounts which is considerably larger than realized; based on the low catches in salmon gill nets and other gear, however, the population is either highly dispersed or inhabits an environment poorly sampled in most studies.

Specific findings which would invalidate this proposed life history of pelagic armorhead include genetic evidence of more than one species in the North Pacific, evidence of spawning in the fat type population, the occurrence of lean and intermediate type preadult stages, or evidence that fat type individuals are physiologically incapable of changing into the intermediate type.

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1. INTRODUCTORY REMARKS

The rapid expansion of tuna fisheries into previously under-exploited oceanic regions, the extension of national jurisdiction of fisheries by most coastal states and the increase in effort in historic fisheries have placed new demands on the management of tuna resources. The subject of how research can respond most effectively to these changes was recently discussed by an international group of research scientists and administrators (Joseph and Wild 1984). A recommendation of that group was that the movements of tunas and their resulting distributions was one of the key biological problems in the management of tuna fisheries and that this problem was so large that the resources of a single organization were insufficient to make rapid progress in solving it.

In order to conceptualize the problem and to define specific research projects and experimental designs for the study of tuna movement dynamics, three technical workshops were held in 1985. The subjects of discussion were as follows: first workshop, the results and uncertainties in conventional mark and recapture studies of tunas; second, the relation between oceanography and tuna movements; and third, new technologies that might be used to measure tuna movements. In these three workshops experts in various fields participated along with a panel. Different experts participated in each of the three meetings (see List of Experts in Annex), but some panel members were present at all meetings and they wrote the final report.

These meetings were supported jointly by the Inter-American Tropical Tuna Commission (IATTC) and the Southwest Fisheries Center (SWFC) of the U.S. National Marine Fisheries Service. The Office de la Recherche Scientific et Technique Outre-Mer (ORSTOM), France, and the South Pacific Commission (SPC), New Caledonia, also contributed to their organization. We wish to acknowledge all the experts who contributed their time and knowledge and many staff members of the IATTC and SWFC who helped with the conduct of the meeting.

The report does not pretend to make research policy for the tuna research community at large, but it draws attention to the opportunities to expand our knowledge of tuna movements and will facilitate discussion of research approaches.

2. STATEMENT OF THE PROBLEM

2.1 Introduction

Most tuna species in the world's oceans are extremely wide ranging. For many it is known, and for others it is presumed that, within a stock[1], individuals migrate rapidly and broadly, so that in the course of one year they can appear in tropical and temperate waters of the high seas and of several management jurisdictions. Few of these movements are sufficiently documented for the purposes of stock assessment and management, yet under the terms of the recent session of the conference on law of the sea most countries are obligated to develop rational management plans that take into account tuna movements.

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[1] In this document we use the term stock in a purely operational or fishery context. We make no judgement on the degree of genetic interchange, differentiation and isolation which are difficult to measure and have interpretations which are dependent on the resolving power of the measurement technique. Usually fishery stocks are assumed to have similar life history characteristics (growth, spawning location and timing, and mortality) although this need not always be the case, nor is it always known to be the case.

Some of the uncertainties respecting tuna movement and distribution are: 1) timing, extent, directionality and seasonality of movements and, in the case of some species, whether stocks undergo directed or seasonal movements at all, 2) rates of exchange of exploitable adults among management jurisdictions and among vertical and horizontal habitats fished by different gears in the same management jurisdiction, 3) distribution of exploitable adults from individual stocks, 4) duration of residence in an area and probability of return to an area, and 5) underlying relationships between environmental factors and tuna movements and distribution.

As a result of these uncertainties it is difficult to choose catch and effort data that are representative of a stock for purposes of stock assessment and to measure the impact of one fishery's catch on the catch of another fishery. These constraints hinder development of rational fisheries policies to maximize economic returns from the overall resource (and portions of it) that occur within individual management jurisdictions.

In the following seven examples we illustrate how present knowledge of tuna movements has been incorporated into tuna management schemes, and how increased knowledge could lead to improved stock assessment and improved management.

2.2 Eastern Atlantic Yellowfin, Thunnus albacares

The status of this stock has been reviewed annually since 1971 by scientists in the Standing Committee for Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT).

When the eastern Atlantic surface fishery for yellowfin was operating in the inshore area (Figure 1, upper), the SCRS (ICCAT 1975) concluded that the maximum sustainable yield (MSY) was equal to approximately 50,000 metric tons and that the corresponding optimum effort (60,000 days) was reached by the 1973 fishery (Figure 2). After 1974, the fishery expanded offshore (Figure 1, lower) and effort increased. As a result the MSY estimated by the SCRS changed (Figure 2, upper) to 110,000 metric tons which could be taken with an effort of 240,000 fishing days. Optimum effort was estimated to be four times the earlier estimate.

This apparent contradiction arose because of a lack of knowledge of stock structure and movements. Eastern Atlantic yellowfin probably consist of a single stock, at least for the purpose of management. However, different sizes of yellowfin differ in their geographical distribution and seasonal movement patterns (young fish inshore, older fish offshore; Fonteneau 1982) and mixing is not uniform between adjacent areas (Fonteneau 1982). These factors biased the conclusions of the initial stock assessment, because at that time the fishery did not cover the entire geographic range of the stock, nor did it exploit all vulnerable size classes.

A similar problem also exists in the vertical dimension for the large yellowfin of the eastern Atlantic. On the basis of production model analysis for large yellowfin caught by longline, the SCRS (ICCAT 1973) concluded in the late 1960's that the eastern Atlantic stock of large yellowfin was producing at the MSY (Figure 2, lower). Then a purse seine fishery developed for large yellowfin in the same waters fished by long line. Between 1965 and 1985 the combined catch of large yellowfin by purse seine and longline greatly increased, and the sustained catch of large yellowfin by surface fisheries was 3.4 times the old estimate of MSY! Interestingly, the size of the fish exploited by the two gears was identical and yield-per-recruit analysis showed that the increased catch could not have been a consequence of increased yield per recruit (Fonteneau 1982). The current explanation for these findings is that the surface component of the large yellowfin stock usually does not mix with the deeper

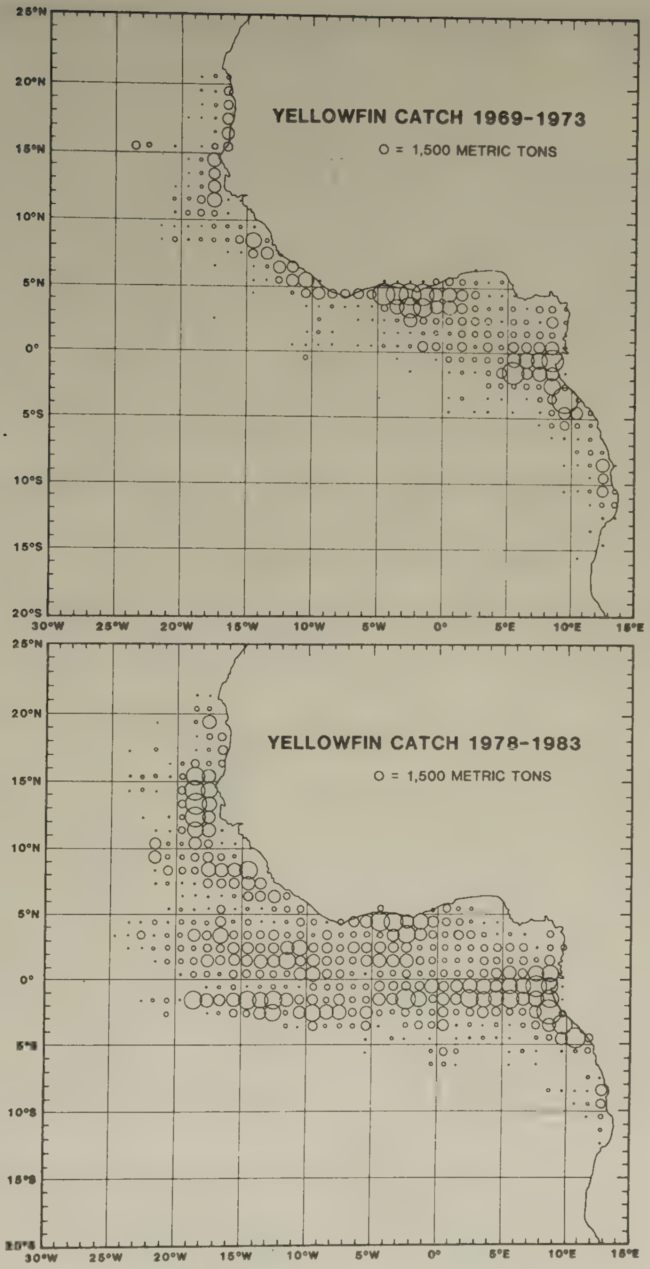

YELLOWFIN CATCH 1969-1973
O = 1,500 METRIC TONS
YELLOWFIN CATCH 1978-1983
O = 1,500 METRIC TONS
25°N
20°N
15°N
10°N
5°N
0°
5°S
10°S
15°S
20°S
30°W
25°W
20°W
15°W
10°W
5°W
0°
5°E
10°E
15°E

Figure 1. Upper; fishing area in the eastern tropical Atlantic during the early fishery (1962 to 1974), shown by the average yellowfin catches of surface fleets from 1969 to 1973. Lower; fishing area in the eastern tropical Atlantic during the recent fishery shown by the average yellowfin catches of surface fleets from 1978 to 1983. The area of a circle is proportional to the catch. Data are from ICCAT statistical data base.

ATLANTIC YELLOWFIN CATCH AND EFFORT

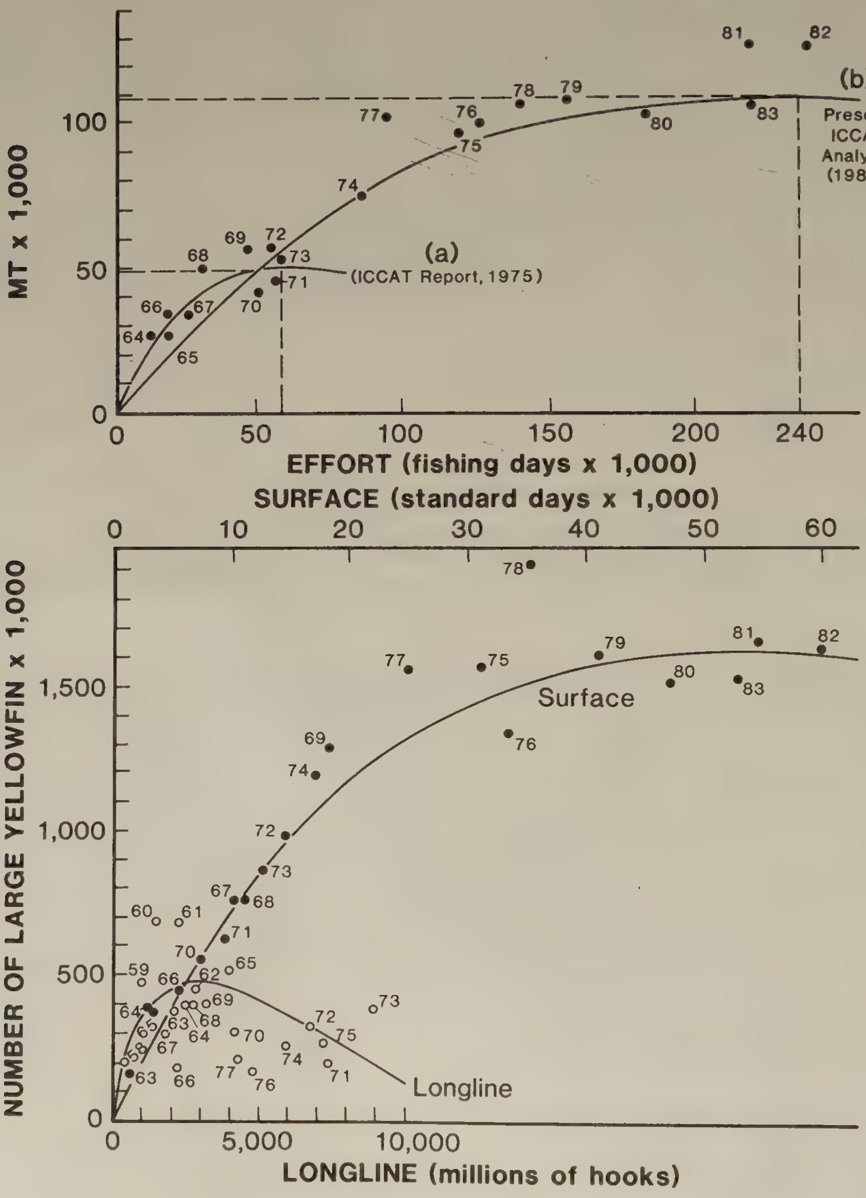


Figure 2. Upper; production model analysis and estimated maximum sustainable yield (MSY) for eastern Atlantic yellowfin tuna, calculated from the 1963-1973 data (ICCAT 1975) and from the 1963-1983 data (present ICCAT analysis). Lower; MSY for large Atlantic yellowfin (in number of fishes calculated for longline fishery (1958 to 1977) and for surface fisheries (1964 to 1983). Data are from ICCAT statistical data base.

component taken by longline vessels in the same area. Clearly, more information is needed on the movement dynamics of Atlantic yellowfin in vertical and horizontal planes before these problems can be solved.

2.3 Northern Atlantic Bluefin, Thunnus thynnus

The northern Atlantic bluefin have two spawning grounds, one in the Mediterranean Sea and one in the Gulf of Mexico. The western and eastern Atlantic spawning groups are believed to be separate stocks, although some juveniles and adults of both groups are known to have made trans-Atlantic migrations (ICCAT 1985). The stock in the western Atlantic is thought to be seriously depleted, while the stock in the eastern Atlantic is also thought to be depressed, but to a much lesser extent (ICCAT 1985). If interchange across the ocean is limited and fish always use the spawning ground of their origin, the catches in the western Atlantic should be greatly reduced to permit the western stock to increase. On the other hand, if considerable interchange of reproducing fish exists, then modest curtailment of the fisheries on both groups would be in order.

Current regulations are based on the assumption that eastern and western Atlantic bluefin constitute separate stocks, and as a consequence quotas apply only to the more seriously depleted western Atlantic fishery. It is not clear that regulations or models that assume no mixing are appropriate since juveniles and adults make trans-Atlantic migrations. Considerably more data from tagging (to measure exchange rates) and estimates of residence times of individual fish using chemical analyses of vertebrae (see section, Reconstruction of Movement Histories from Microconstituents of Mineralized Tissue) may help resolve this issue.

2.4 Southern Bluefin, Thunnus maccoyii

Southern bluefin appear to have a circumpolar distribution south of 30° S (Figure 3) but the rates of exchange of bluefin among the different fisheries and fishing areas remain unknown. Tagging and catch data indicate that southern bluefin move south and east from the only known spawning area in the eastern Indian Ocean off the northwest coast of Australia, and appear at progressively older ages (2 through 6 years) in the Western Australia, South Australia, Tasmania and New South Wales fisheries (Murphy and Majkowski 1981) (Figure 4, upper). Bluefin tagged off South Australia have also been recovered well to the west in the Japanese longline fishery off the south coast of Africa (Figure 4, lower). However, the numbers of juvenile bluefin (ages 2-6) that move from Australia in a westerly or easterly direction through the southern ocean, in the area of the west wind drift, are not indicated by the pattern of tag recoveries and longline catch information (Olson 1980). Also unknown are the patterns and frequency of return migrations by bluefin over their 15-20 year life span to the single Indian Ocean spawning area.

The total world catch of southern bluefin has declined from 81,000 metric tons in 1965 to about 35,000 mt in 1984 (Figure 5). Cohort analysis indicates that the world standing stock underwent a dramatic decline from 1960 to the early 1970's and that recruitment had been impaired by low parental stock levels of recent years (Murphy and Majkowski 1981).

The widely distributed Japanese longline fishery (Figure 4, upper, inset) and the Australian surface fisheries for younger fish (Figure 4, upper) take 95% percent of the world harvest of southern bluefin. Australia implemented a management plan for the 1983/1984 fishery to stabilize the level of the southern bluefin stock at the estimated 1980 level of abundance. The plan included an overall catch quota for Australian

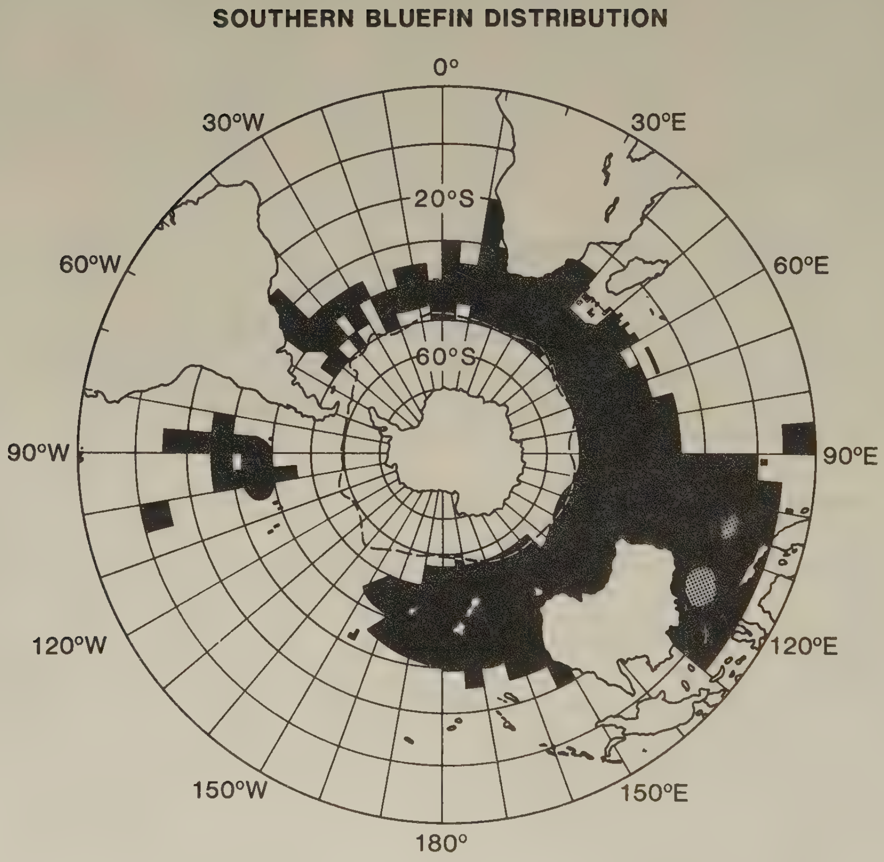

SOUTHERN BLUEFIN DISTRIBUTION
0°
30°W
30°E
20°S
60°W
60°E
60°S
90°W
90°E
120°W
120°E
150°W
150°E
180°

Figure 3. Distribution of southern bluefin tuna (after Harden Jones 1984, with additional data from Shingu 1967 and Hynd 1969 (in 1° areas); Fisheries Agency of Japan 1974, 1975, 1976, 1977, 1978, 1979 (in 5° areas); and Suda 1971, Robins 1963, and Nakamura 1969). The dashed line marks the Antarctic Convergence. The stippling marks the known breeding areas.

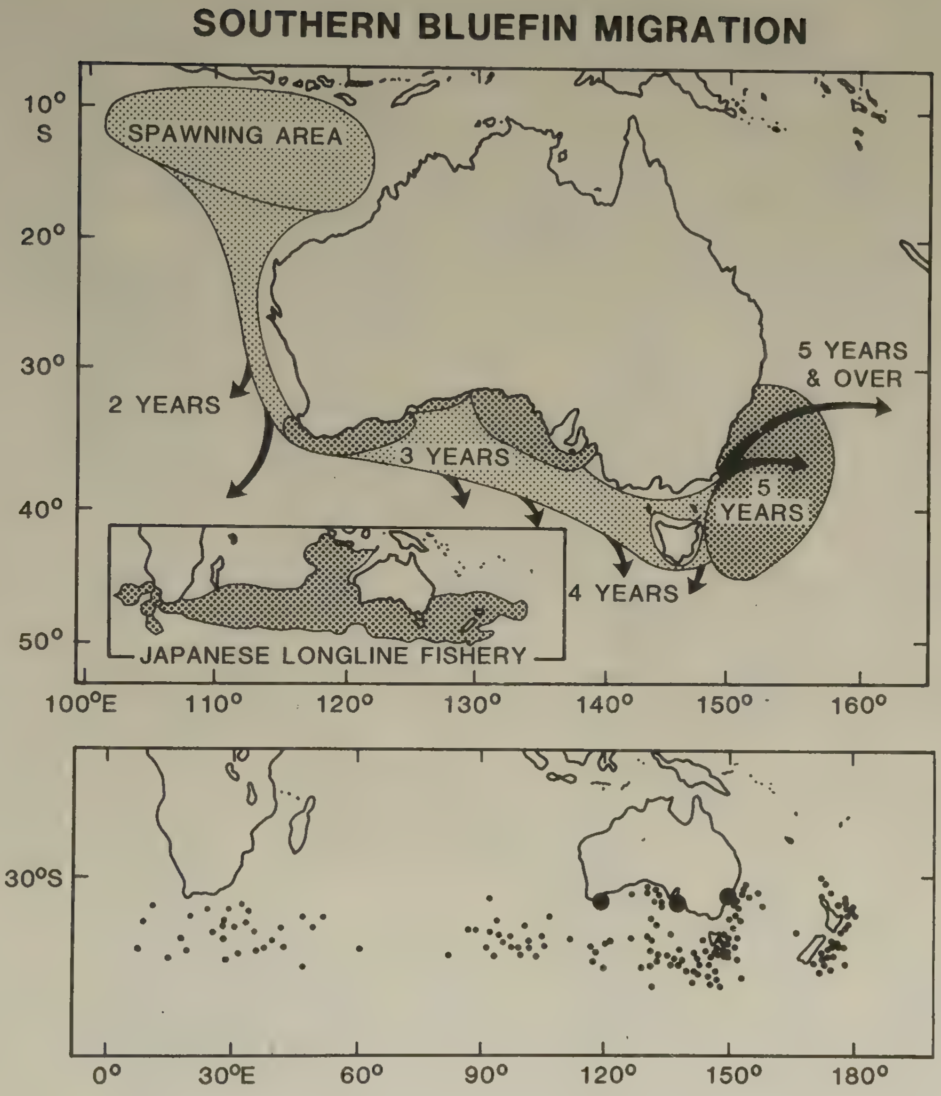

SOUTHERN BLUEFIN MIGRATION
SPAWNING AREA
10°
S
20°
30°
40°
50°
2 YEARS
3 YEARS
4 YEARS
5 YEARS
5 YEARS
& OVER
JAPANESE LONGLINE FISHERY
100°E
110°
120°
130°
140°
150°
160°
30°S
0°
30°E
60°
90°
120°
150°
180°

Figure 4. Upper; southern bluefin tuna spawning area and migration pattern off Australia (shown in light stippling). Dark stippling shows the operation areas of the Australian fishery and the Japanese longline fishery (inset). Arrows indicate the direction of fish migration from the Australian fishery. Lower; locations where fish tagged off Western Australia, South Australia, and New South Wales were recaptured after more than one year of liberty (after Murphy and Majkowski 1981).

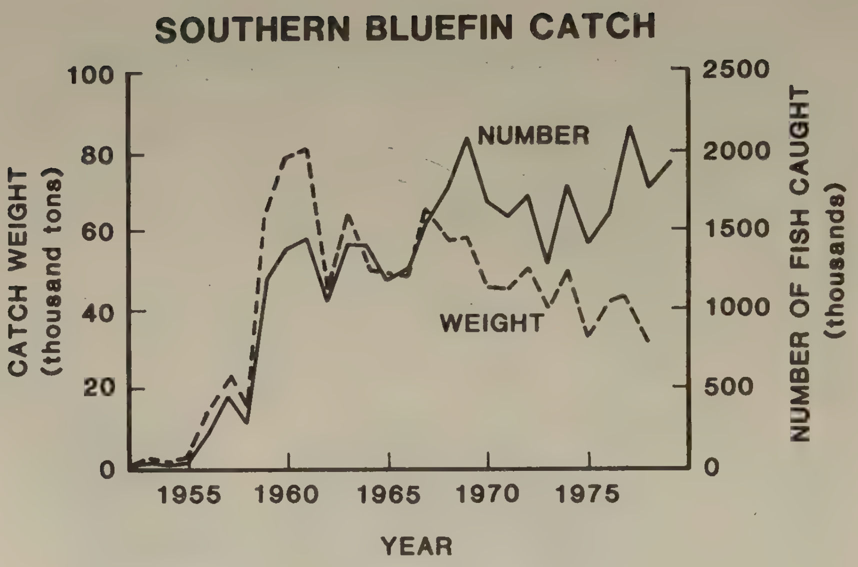


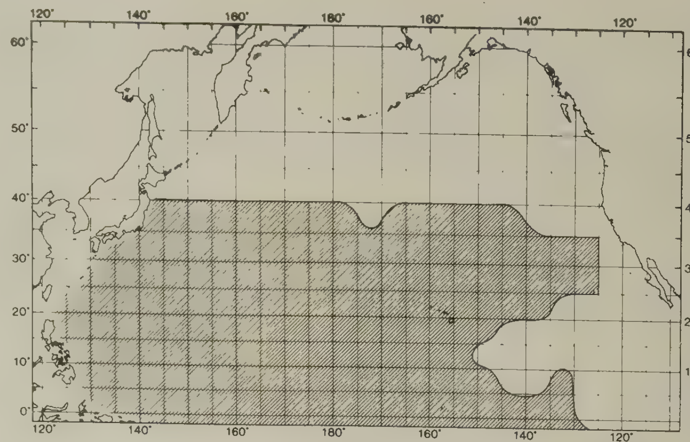
Figure 5. The history of the total catch of southern bluefin tuna (after Murphy and Majkowski 1981).

fisheries of 19,000 metric tons, with specific allocations to fisheries in Western Australia and South Australia (Franklin and Burns 1983). The high-seas longline fishery of Japan has not been placed under catch limits.

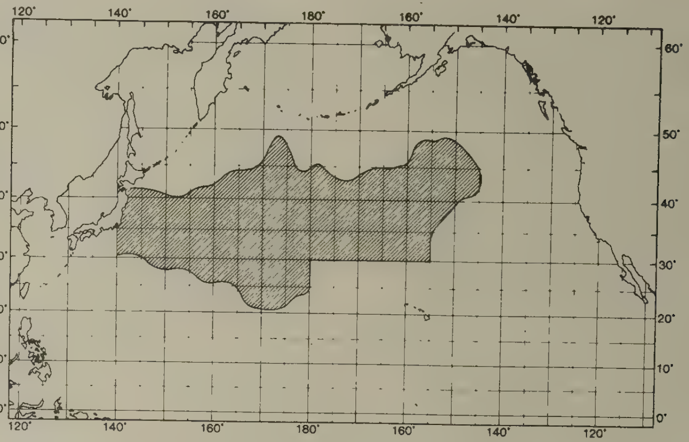
Clearly a major uncertainty in assigning catch limits to specific fisheries of southern bluefin is the extent that the catch in any one fishery reduces catches by other fisheries along the bluefin migration route. In addition, migration patterns and frequency of return migrations by bluefin to their Indian Ocean spawning area need to be better defined.

2.5 North Pacific Albacore, *Thunnus alalunga*

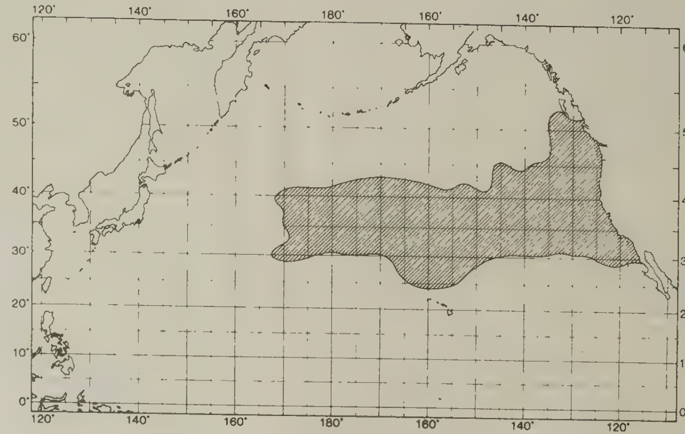
A growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs and Weatherall 1981) indicates that albacore in the North Pacific are not as homogeneous as previously assumed (Clemens 1961; Otsu and Uchida 1963). Results from recent tagging suggest that north Pacific albacore may consist of two stocks that have different migratory patterns (Laurs et al. 1979). Fish belonging to a proposed northern north Pacific stock migrate between the eastern and western north Pacific, resulting in an interchange of fish of unknown magnitude between the U.S. fishery north of 40° N, the Japanese live bait and gillnet fisheries, and the Asian longline fisheries west of 180° (Figure 6). Fish belonging to the proposed southern north Pacific stock have a different migration route than those of the northern north Pacific stock. These fish enter the U.S. fishery south of 40° N and the longline fisheries east of 180°. Only a small proportion of the proposed southern north Pacific stock appears to migrate between the eastern and western Pacific to enter the Japanese fisheries. Also, during a particular fishing season, little exchange of albacore exists between the proposed northern and southern stocks that are exploited by the U.S. fishery. There is, however, a small amount of interannual exchange. An analogous situation to that posed above may also exist for albacore in the north Atlantic Ocean (Delaporte 1982).


120°
140°
160°
180°
160°
140°
120°
60°
50°
40°
30°
20°
10°
0°

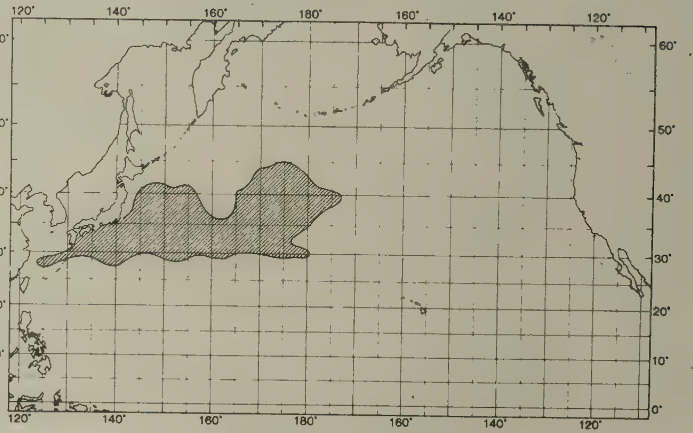
1980 JAPANESE LONGLINE


120°
140°
160°
180°
160°
140°
120°
60°
50°
40°
30°
20°
10°
0°

1981 JAPANESE GILLNET


120°
140°
160°
180°
160°
140°
120°
60°
50°
40°
30°
20°
10°
0°

1983 U. S. SURFACE FLEET


120°
140°
160°
180°
160°
140°
120°
60°
50°
40°
30°
20°
10°
0°

1979 JAPANESE POLE & LINE

Figure 6. Catch areas of the four major fisheries for North Pacific albacore (from Majors et al. 1984).

Tagged north Pacific albacore recaptured off the coast of North America north of 40° N and in the western north Pacific off the coast of Japan grow more slowly than those recovered off the coast of north America south of 40° N (Laurs and Wetherall 1981). The differences in growth rate were consistent with differences in length frequencies of albacore caught north and south of 40° N (Brock 1943; Laurs and Lynn 1977).

Clearly, the situation for north Pacific albacore is complex and dynamic, with each stock's contribution to each fishery varying from year to year. Some evidence exists that such variation is directly linked to changes in oceanographic conditions (Laurs pers. comm.). Confirmation that more than one stock was present in north Pacific albacore fisheries would have important consequences for stock assessment, fishery evaluation, management policy, and development of accurate catch forecasting systems. Thus further work is needed on movements of albacore to clarify stock structure and migratory exchange.

2.6 Eastern Pacific Yellowfin, *Thunnus albacares*

In 1961 the Inter-American Tropical Tuna Commission (IATTC) proposed a catch quota of 83,000 short tons of yellowfin to conserve the stock in the eastern Pacific. No boundaries for the stock were defined and no regulation resulted. In 1962, the Commission defined a Yellowfin Regulatory Area (CYRA) (Figure 7) which included all areas of the eastern Pacific where the surface fishery existed and a large offshore area where no fishery existed except in the vicinity of a few distant islands (IATTC 1963:15). In the mid and late 1960's many newly-constructed large purse seiners began to fish further offshore and in 1968 they began to fish outside the CYRA. Within a few years some had extended their operations as far west as 150° W, making it possible to better establish the western boundary of the CYRA. Subsequent tagging of yellowfin inside and outside the CYRA (Bayliff 1979) showed relatively little interchange of fish across the boundary, but these data were of relatively poor quality because of low tag return rates and lack of year-round fishing both inside and outside the CYRA. Length-frequency studies have shown that the fish outside the CYRA tended to be larger than those inside the CYRA (IATTC 1985: Figures 13 and 14). After the fishery had been regulated for several years it became apparent that little fishing existed in some of the more remote portions of the CYRA and several of these were designated as "experimental areas" (Figure 7) where unrestricted fishing was permitted experimentally.

No international regulations for yellowfin fishing have existed in the eastern Pacific since 1979. If and when regulations are required, a need will exist to better define size-specific movements of yellowfin within and outside the CYRA. Experimental areas will probably continue to be designated so that regulations can be adjusted in accordance with the latest knowledge of yellowfin movement.

2.7 South Pacific Skipjack, *Katsuwonus pelamis*

Prior to the program of the South Pacific Commission (SPC) on abundance and movements of skipjack in the central and western Pacific, two-stock (Fujino 1972, 1976) and five-stock (Sharp 1978) hypotheses of skipjack stock structure in the Pacific existed. On the basis of geographical distributions presented for these stocks, the two hypotheses had been used to support the management policies of particular groupings of countries (Kearney pers. comm.). Several of the proposed stock boundaries fell within the SPC (Figure 8) and IATTC (Figure 7) areas, and many skipjack tagged by these agencies were recovered after crossing the boundaries (SPC 1981) proposed by Fujino and Sharp. A clinal hypothesis of stock structure (Richardson 1983) seems a reasonable alternative to the "isolated" stock hypotheses of Fujino and Sharp. The clinal hypothesis is

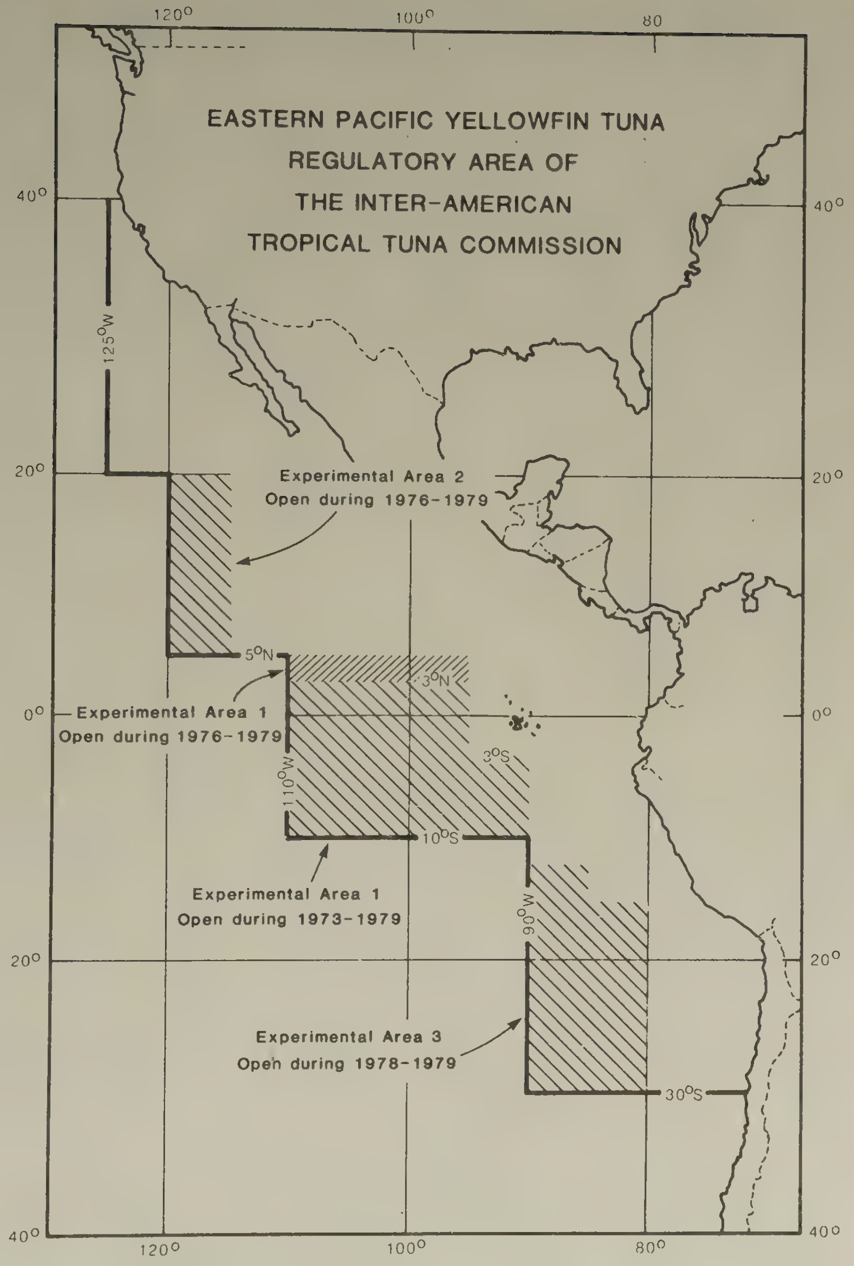

EASTERN PACIFIC YELLOWFIN TUNA REGULATORY AREA OF THE INTER-AMERICAN TROPICAL TUNA COMMISSION
120°
100°
80
40°
20°
0°
20°
40°
125°W
Experimental Area 2
Open during 1976-1979
5°N
3°N
Experimental Area 1
Open during 1976-1979
3°S
110°W
10°S
Experimental Area 1
Open during 1973-1979
90°W
Experimental Area 3
Open during 1978-1979
30°S
120°
100°
80°

Figure 7. The eastern Pacific yellowfin tuna regulatory area of the Inter-American Tropical Tuna Commission (from IATTC 1985). The heavy line is the outer boundary of the CYRA.

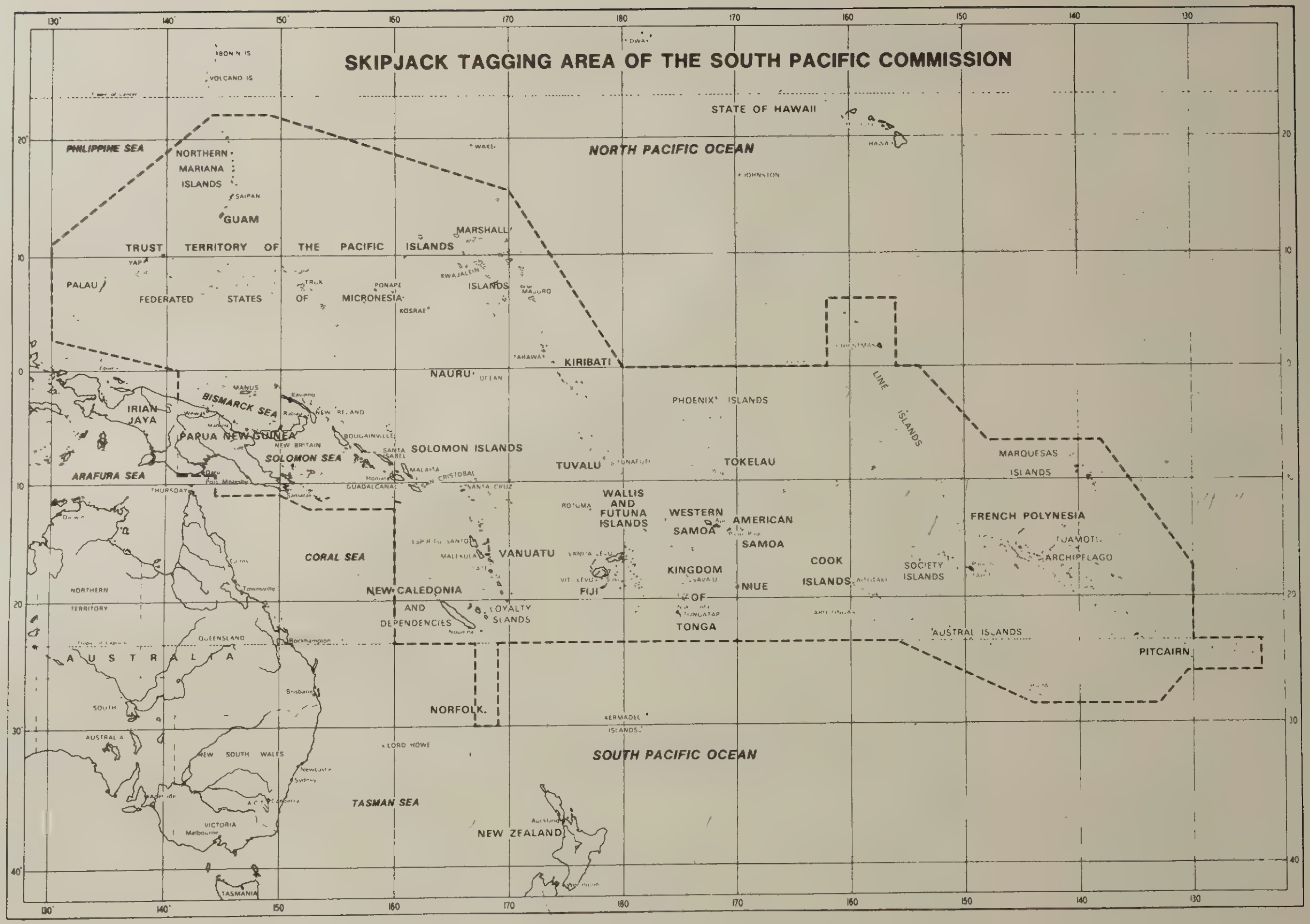

SKIPJACK TAGGING AREA OF THE SOUTH PACIFIC COMMISSION
NORTH PACIFIC OCEAN
SOUTH PACIFIC OCEAN
STATE OF HAWAII
PHILIPPINE SEA
NORTHERN MARIANA ISLANDS
GUAM
TRUST TERRITORY OF THE PACIFIC ISLANDS
MARSHALL ISLANDS
FEDERATED STATES OF MICRONESIA
PALAU
NAURU
KIRIBATI
PHOENIX ISLANDS
LINE ISLANDS
IRIAN JAYA
BISMARCK SEA
PAPUA NEW GUINEA
SOLOMON SEA
SOLOMON ISLANDS
ARAFURA SEA
CORAL SEA
TUVALU
TOKELAU
WALLIS AND FUTUNA ISLANDS
WESTERN SAMOA
AMERICAN SAMOA
VANUATU
FIJI
NEW CALEDONIA AND DEPENDENCIES
LOYALTY ISLANDS
KINGDOM OF TONGA
NIUE
COOK ISLANDS
MARQUESAS ISLANDS
FRENCH POLYNESIA
TUAMOTU ARCHIPELAGO
SOCIETY ISLANDS
AUSTRAL ISLANDS
PITCAIRN
NORFOLK
KERMADEC ISLANDS
LORD HOWE
TASMAN SEA
NEW ZEALAND
AUSTRALIA
NORTHERN TERRITORY
QUEENSLAND
SOUTH AUSTRALIA
NEW SOUTH WALES
VICTORIA
TASMANIA
130 140 150 160 170 180 170 160 150 140 130
20 10 0 10 20 30 40

Figure 8. The skipjack tagging area of the South Pacific Commission (from Kleiber et al. 1983).

supported by the tagging results and a variety of new evidence, including sampling for tuna juveniles and states of sexual maturation (Argue et al. 1983), blood electrophoretic sampling and tagging skipjack from the same schools (SPC 1980, 1981), and analysis of skipjack growth (Sibert et al. 1983).

Unfortunately all lines of research on stock structure of Pacific skipjack had deficiencies (Argue et al. 1986). In the case of tagging data, not knowing the route that skipjack traversed between release and recovery meant that the range and pattern of skipjack movement could not be inferred with great confidence. For example, many fish at large for long periods were recovered near their release locations. These fish may have migrated extensively and then returned (or homed) to the release site or the recaptured fish were local residents and did not migrate at all. Clearly, much greater confidence could be placed on interpretations of tag recovery data if the paths traversed by skipjack were known. Such information would be useful in defining stocks and detecting the effect of one skipjack fishery on another.

Several analytical models (Kleiber et al. 1984; Sibert 1984) have been developed to quantify interactions between skipjack fisheries using the tag and recovery data collected by the SPC. Interactions were found to be negligible between locally based fisheries in the 200-mile zones of Papua New Guinea, Solomon Islands, Fiji, and New Zealand (SPC 1984a). Results for Japanese distant-water pole-and-line fisheries in the waters of the Republic of Palau, the Commonwealth of the Northern Marianas, the Federated States of Micronesia, and the Marshall Islands (countries where the north equatorial counter current is the dominant oceanographic feature) were more equivocal. There was some indication that skipjack moved in sequence, from west to east through pole-and-line fisheries that operated in the vicinity of the north equatorial counter current. Some estimates of interaction for these fisheries were quite high (SPC 1984).

Subsequent to this work the skipjack catch increased greatly and the distribution of fishing effort changed as more and more purse-seiners entered the fishery and distant-water pole-and-line vessels began to be phased out. Although the early tagging results suggested that there was not much interaction between pole-and-line fisheries, there was concern that these data did not accurately represent the situation, where purse-seine, pole-and-line and artisanal fisheries operated together. There was also concern that seasonal and directed movements of skipjack might not have been detected in the original tagging study due to inadequacies of experimental design.

On a finer scale, the purse-seine, local artisanal and local pole-and-line fisheries have come to depend heavily on anchored fishery aggregation devices that concentrate surface tunas and apparently make them more vulnerable to hook-and-line gear. The available conventional tagging data provide little information on the optimum distribution and numbers of devices to employ to maximize catches and minimize costs. Ultrasonic tracking of skipjack holds promise for solving this problem.

The skipjack resource is of great economic importance to the small countries of the central and western Pacific (Kearney 1979), and considerable fishing pressure exists in their waters as well as in international waters. Their combined 200-mile zones cover over one half of the ocean area west of 175° E. If it is found that large numbers of skipjack consistently move through a series of fishing areas in seasonal sequence and that fisheries at the end of the series are most severely affected by low catch rates, then such a finding would have important consequences for developing fishery policy in this region. This clearly is an area where further research on skipjack movement is warranted.

2.8 Atlantic Bigeye, *Thunnus obesus*

In the eastern Atlantic, bigeye tuna are exploited by fisheries in widely separated areas from the equator to temperate waters. Each fishery takes a different size class of bigeye: very small bigeye (<5 kg) are taken by bait boat and purse-seine in the Gulf of Guinea; 5 to 15 kg bigeye are caught by bait boat in tropical waters off Senegal and Mauritania; and large bigeye (>15 kg) are captured by longline and bait boat in temperate waters, such as those off the Canary Islands and off the Azores (ICCAT 1984a; Figure 9).

It is assumed that bigeye migrate from their equatorial spawning area to foraging areas that end in temperate waters (ICCAT 1984). During this migration they pass through 200-mile zones of many countries (and through international waters), where they are exploited by different gears. In each of these fisheries the estimates of yield per recruit will, of course, differ since parameters of growth and mortality differ in each zone (Pereira 1984). Rational management of the bigeye resource must take into account these movements and associated changes in productivity as bigeye move through fisheries with different harvest levels.

2.9 Conclusions

The new Law of the Sea has placed an obligation on coastal- and distant-water fishing nations to develop rational management plans for harvesting exploitable fishery resources. The seven examples described here illustrate how weaknesses in the understanding of distribution and movement of the principal tuna species have constrained development of rational management policy for many fisheries.

These weaknesses are often revealed when it is necessary to develop management plans or select catch and effort data that is representative of the stock after the fishery has expanded into a new area. This problem has become particularly important for management of depressed bluefin stocks. Another problem area is the quantification of interchange of fish between fisheries in different management jurisdictions and between gear types in the same jurisdiction. This area is presently of great importance to management of the yellowfin, Pacific skipjack and southern bluefin stocks, and will take on increasing importance with all tuna stocks as fisheries expand. On a finer scale, interchange of tuna among fish aggregating devices needs to be determined to optimize deployment strategies.

To make a fundamental advance in resolving these uncertainties and the other management problems we have discussed will require better information on the movement dynamics of tunas. Fishery-independent estimates of distribution and movement of exploitable adults are needed, as is knowledge of internal (physiological) and external (environmental) mechanisms governing their movement that could improve the predictability of movements. These issues are considered in the next sections.

3. PRESENT APPROACHES

In this section we discuss the research approaches and technologies presently used to describe the migrations and movements of tunas and to study the mechanisms underlying them. We describe the use of fishery information and mark and recapture data to measure tuna movements, discuss the movements of tunas in relation to oceanographic conditions, describe how a synthesis of existing data might expand our knowledge of movements, and discuss the use of a relatively new technique, ultrasonic telemetry. In this process, we attempt to identify the benefits and limitations of specific technologies and point out ways traditional approaches can be used in the future to expand our knowledge of tuna movements.

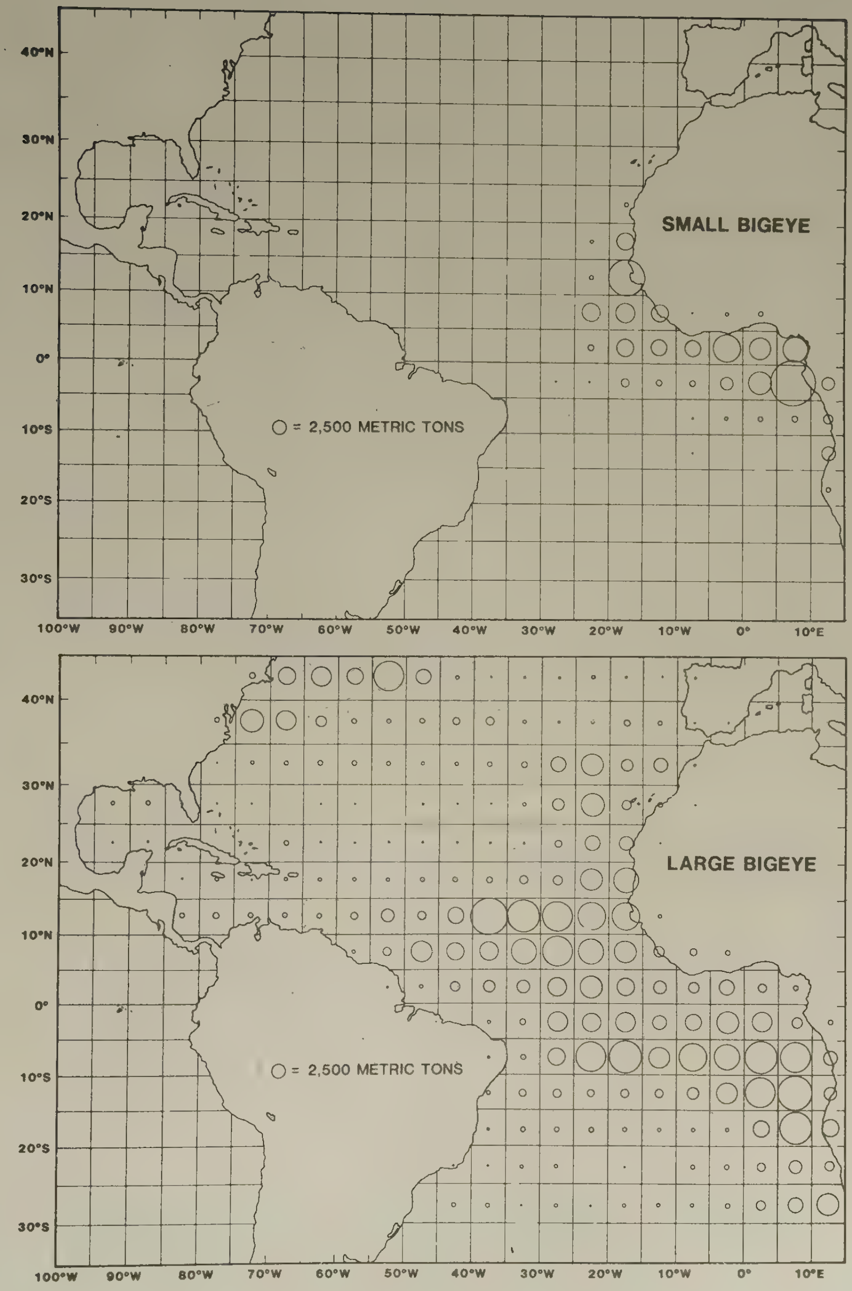

SMALL BIGEYE
○ = 2,500 METRIC TONS
LARGE BIGEYE
○ = 2,500 METRIC TONS
40°N
30°N
20°N
10°N
0°
10°S
20°S
30°S
100°W
90°W
80°W
70°W
60°W
50°W
40°W
30°W
20°W
10°W
0°
10°E

Figure 9. Upper; average catch of small bigeye (≤ 15 kg) by purse-seiners from 1975 to 1982. Lower; average catch of large bigeye (> 15 kg) by longliners from 1975 to 1982. The area of a circle is proportional to the catch. Data from ICCAT statistical data base.

3.1 Tuna Movements From Fishery Information

Many examples exist of the movements of tuna originally inferred from fishery statistics and later confirmed with tagging. The oldest reference is probably that of Aristotle (1910) who described fairly accurately the migrations of the Mediterranean bluefin tuna 20 centuries ago, using the spatial and temporal distribution of the catches. More recently, hypotheses regarding the movements of Atlantic yellowfin were made from catch and catch and effort data from surface and longline fisheries (Richards 1969; Honma and Hisada 1971) before any tagging was done.

Reasonable hypotheses for the movements of most of the world's tuna stocks can be inferred from fishery data provided: 1) the fisheries exploit most of the stock -- sizes and distribution; 2) reasonably good catch and length frequency data (small time and area resolution) are available; and 3) the species show consistent annual distribution patterns (true for most tunas).

Although changes in the vulnerability to capture may be misinterpreted as migration, in general fishery statistics are still useful for formulating hypotheses about tuna migrations. The relatively "recent" development of more active and powerful techniques, such as tagging and telemetry, will not replace, but rather complement, this traditional approach, and fishery statistics will remain an important source of information for the studying of the movements of tuna in relation to their environment because of the extensive data available and wide geographic coverage. Improved precision of the data, which in some cases permits analysis on a temporal scale of days, and a spatial scale of minutes of latitude and longitude (Fonteneau 1978) offer new opportunities for the study of tuna movements using fishery statistics. Improved computer facilities and graphical displays will facilitate such analyses. New work can be done on size-specific movements as length data become available.

3.2 Marking and Recapture of Tunas

Analysis of the recoveries of marked tunas combined with fishery information has provided most of our knowledge of tuna migrations and movements. However, the greatest advances have been made when mark and recapture data were combined with other information, such as larval distributions and the results of length-frequency analyses and biochemical and morphometric studies (Argue et al. 1983; Bayliff 1983). The method of marking and recapture also provides estimates of natural and fishing mortality, growth, stock structure, and schooling behavior, as well as defining migrations and exchange rates among fisheries, making it one of the most powerful methods for acquiring information needed for tuna management.

3.2.1 Mark and Recapture Methodology

Tags have been applied to tunas caught by baitboats, trollers, sport-fishing boats, purse seiners, traps, and other gear. About 607,000 tunas have been marked with conventional tags, mostly from baitboats. Streamer tags were used during the 1950's, but these were replaced during the 1960's by dart tags with nylon or steel heads, the latter being used for larger tunas captured by recreational fishermen and tagged while in the water. Most of the tunas that have been tagged have been skipjack or yellowfin tuna, but substantial numbers of all the important species have been tagged. The largest number of fish tagged in one day on a single vessel was 3,689 (skipjack, mean length 48 cm; Argue and Kearney 1983). The tags are usually returned by fishermen, unloaders, and cannery workers who receive modest rewards for returning tags and in some cases chances to win substantial cash prizes in drawings held at the end of the year (ICCAT

1983: 218-219). In many cases, employees of fishery organizations make daily visits to tuna unloading areas to collect the tags found by the workers.

3.2.2 **Movements**

Past studies of the transoceanic movements of bluefin tuna illustrate the crucial role of mark and recapture data and the importance of ancillary information used to interpret such data. Godsil and Byers (1944) concluded from an analysis of anatomical characteristics that two species of northern bluefin existed in the north Pacific, but this hypothesis was later rejected when fish tagged in the eastern Pacific were recaptured in the western Pacific and vice versa (Clemens and Flittner 1969). Similarly, the eastern and western Atlantic bluefin were considered separate species (Ginsburg 1953) until subsequent tagging showed that transoceanic migrations in both directions existed (Mather and FAO, 1972). In the north Pacific, bluefin spawning occurs only in the vicinity of Japan (Bayliff 1980), indicating all fish in the eastern Pacific have migrated across the ocean. On the other hand, in the Atlantic, transoceanic spawning migrations cannot be inferred because larval data indicate spawning occurs on both sides of the Atlantic (Mediterranean Sea and the Gulf of Mexico). Recent analyses of the chemical composition of the vertebrae seem to indicate that only a minority of bluefin cross the Atlantic Ocean (Calaprice 1986).

Tagging experiments indicate that during the annual migration of albacore across the northeastern Pacific to North America virtually no interchange exists between albacore north and south of 40°N latitude and only a low rate of interchange across that boundary occurs at other times (Laurs 1983). Other studies (Laurs and Wetherall 1981) indicate that the growth rates of fish from the two areas differ.

Mark and recapture studies have also shown that considerable mixing of yellowfin exists in the Pacific Ocean. Yellowfin seem to move long distances less frequently (Fink and Bayliff 1970; Bayliff 1979) than do bluefin or albacore, and little or no evidence of homing exists for yellowfin. Nevertheless studies of the distribution of adults and larvae, sexual maturity, length frequencies, and tag returns of yellowfin suggest that three stocks may exist in the Pacific (Suzuki et al. 1978).

Considerable mixing of skipjack exists in the Pacific Ocean. Skipjack, like yellowfin, move long distances less frequently (Fink and Bayliff 1970; Kleiber et al. 1983) than do bluefin or albacore, but their migration from the eastern to the central and western Pacific as the fish approach maturity (IATTC 1983: 32-33) suggests homing. Extensive ichthyoplankton surveys have produced few skipjack larvae in the eastern Pacific, and large skipjack make up a much higher portion of the catch in the central relative to the eastern Pacific. These facts have led investigators to believe that the skipjack in the eastern Pacific are hatched from eggs spawned in the central and western Pacific (Rothschild 1965).

The net distances traveled by yellowfin tagged in the eastern Pacific and skipjack tagged in the western Pacific after 0-30,31-180, and more than 180 days at liberty are shown in Figure 10. It is obvious that many of the fish moved considerable distances from the locations of release. Most of the tagging took place in areas where fishing effort was heavy. If the fishing effort were evenly distributed in the Pacific Ocean there probably would have been fewer returns of fish which had moved short distances and more returns of fish which had moved long distances.

An important uncertainty is the extent that the apparent dispersion of fish from a tagging site is an actual representation of their movement

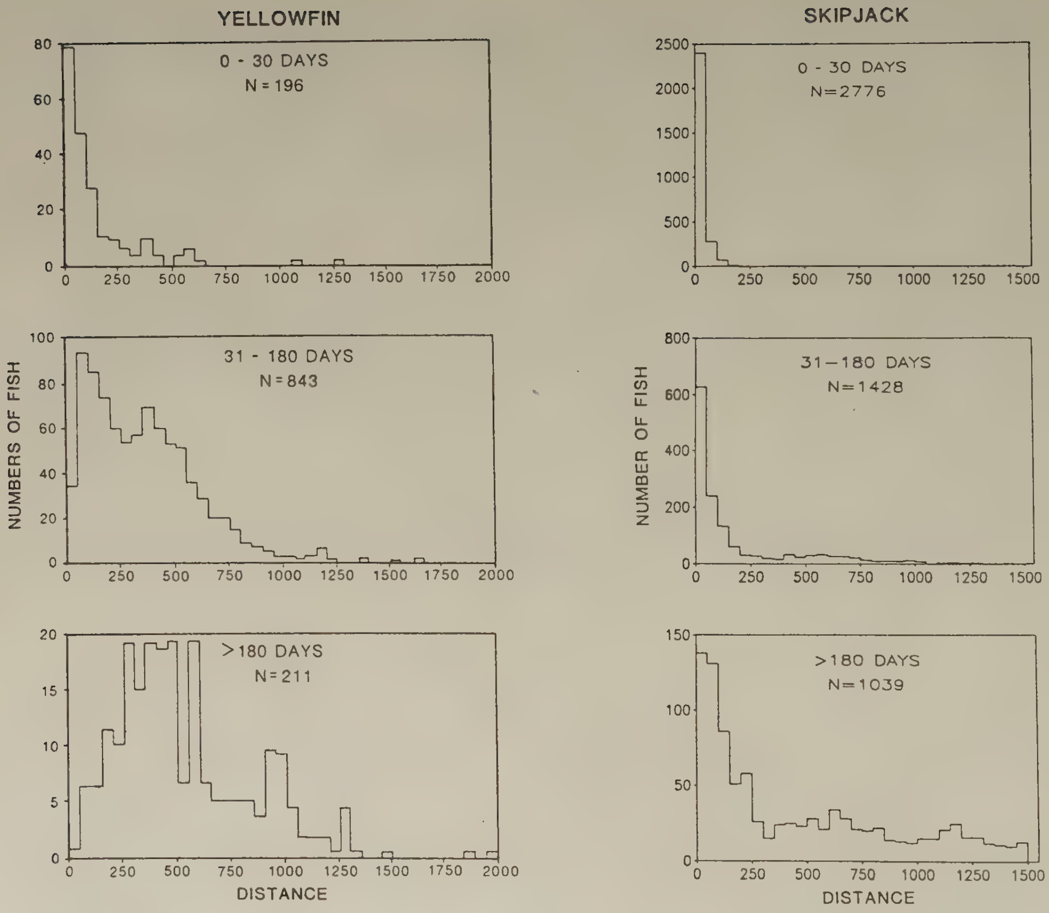


Figure 10. Net distances, in nautical miles, traveled by purse seine-caught yellowfin tagged in the eastern Pacific during 1968-1978 (W.H. Bayliff, pers. comm.) and baitboat-caught skip tagged in the western Pacific during 1977-1980 (after Ke y 1983). One yellowfin, not shown in the figure, was recap d 2,765 miles from the point of release after 138 days at lib rty.

rather than an artifact of the present marking and return system. Obviously many of the biases and constraints in mark and recapture technology could lead to erroneous conclusions about the movements of tuna. These are discussed in more detail in subsequent sections. Clearly, better knowledge of the actual paths followed by the fish for extended periods is needed before these issues can be resolved.

3.2.3 **Return Rates**

The percentage of tags that are recovered and returned varies widely among and within species, as indicated in Table 1.

Table 1

Percentages of tags returned.

Species	Area	Years	Total percentages of return Min	Max	Mean	Reference
Yellowfin	Eastern Pacific	1959-1964	2.7	65.3	21.6	Fink and Bayliff, 1970
Skipjack	Eastern Pacific	1959-1964	2.3	43.9	8.1	Fink and Bayliff, 1970
Skipjack	Western and central Pacific	1977-1980	0.0	13.9	4.4	SPC, 1984b
Northern bluefin	Western Atlantic	1954-1971	0.0	44.2	23.6	Mather and working party, 1972
Albacore	Eastern Pacific	1971-1978	2.0	8.5	5.4	Laurs and Weatherall, 1981

The great majority of the marked yellowfin and skipjack that have been recaptured were at liberty less than one year, whereas a substantial fraction of marked albacore and bluefin have been recaptured after over one year. In fact, the record time at liberty for a tagged tuna is for a southern bluefin that remained at large for nearly 18 years (Anonymous 1981). The decline in recoveries of marked tunas with time varies not only among species, but also within species. For example, among skipjack fisheries, the decline in recoveries is steepest in the eastern Pacific, intermediate in the eastern Atlantic, and most gradual in the southwestern Pacific (Figure 11). Skipjack from the eastern Pacific migrate to the central and western Pacific prior to spawning, but are seldom recovered by the minor fisheries in those areas (IATTC 1983: 32-33), whereas the southwestern Pacific includes both major fisheries and several major skipjack spawning areas (Argue et al. 1983).

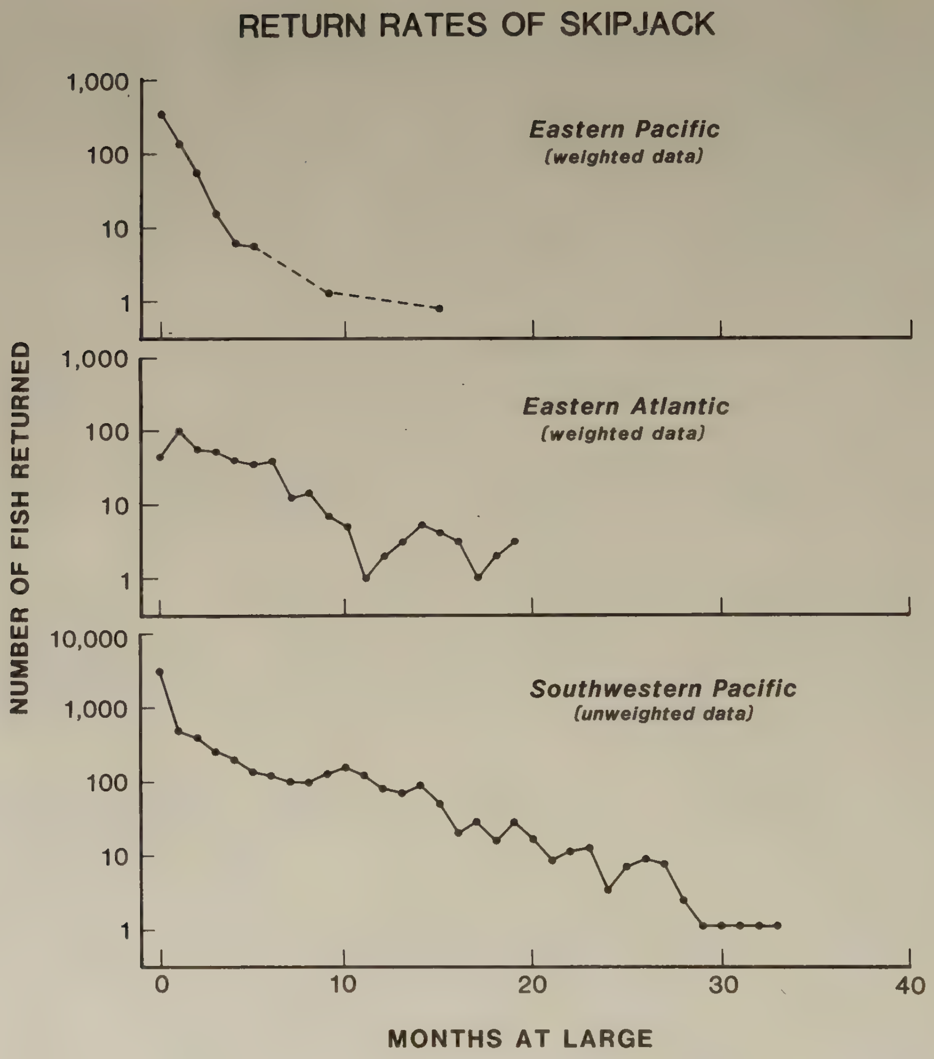


Figure 11. Catch curves for tagged skipjack in the eastern Pacific (Bayliff 1977), eastern Atlantic (Bard et al. 1983), and southwestern Pacific (Kleiber et al. 1983).

3.2.4 Uncertainties and Limits of Conventional Mark-Recapture Technology

Substantial numbers of several species of tuna are caught at sizes in excess of 50 kg, but because of technical problems tunas larger than about 20 kg are seldom tagged. Some tunas tagged when they were small were recovered after having grown considerably, but such events are rare because of high rates of fishing and natural mortality. Thus many small fish must be tagged to ensure the recovery of even a few large ones. For example, in the eastern Pacific surface fishery for yellowfin (where the annual coefficients of natural and fishing mortality are about 0.8 and 0.7, respectively), if 1,000 yellowfin were tagged, one would expect a return of about 363 (36%) of the tags in the first year, 81 (8%) in the second, 18 (2%) in the third, 4 (<1%) in the fourth, and 1 in the fifth. The observed recovery rates, however, after the first year are even lower than those predicted from the natural and fishing mortality rates. Of 13,598 yellowfin tagged off Baja California during 1957-1963, 6,621 tags (49%) were returned in the first year (May-April), but only 73 (1%) were returned in the second year, only 2 (<1%) during the third year, and none thereafter (Bayliff 1971). High vulnerability to capture shortly after tagging, lesser vulnerability to capture of larger fish, and shedding of the tags may be responsible for the differences between the observed and expected returns.

The attrition rate of tag recoveries can be considered as the reduction in the tagged stock with time due to natural and fishing mortality, tag shedding, mortality caused by the tags, growth out of vulnerability to the fishery, and emigration (Kleiber et al. 1983). Ideally, it would be useful to partition attrition into, at least, natural mortality, emigration, and other losses. Cayré, Diouf, and Fonteneau (1986) have estimated the instantaneous rate of mortality due to carrying tags for skipjack. Although no attempt to partition the attrition rates into those classes has been entirely successful (Sibert 1984), some possible research approaches discussed later in this report might ultimately make this problem more tractable.

A number of other problems exist in the interpretation of mark and recapture data in addition to lack of understanding of the relative role of the various factors that affect the attrition rate of tagged fish. It is difficult to be certain that tagged fish are truly representative of a study area, as usually only one or a few vessels are used to capture tunas for tagging, and the released fish may not quickly mix within the study area. In addition, vessels often do not fish in all areas occupied by the stock, and this distorts the apparent movements as indicated by the recapture data. Some adjustments can be made by dividing the numbers of recoveries by the fishing effort in the recovery areas (Bayliff 1979). A more accurate adjustment would be to adjust the recoveries for fishing effort over the actual path followed by the fish between release and recovery, but this is not possible using existing approaches.

The recovery of tags is an additional problem, as some of the finders of tagged tunas do not return the tags or furnish poor data. Bard et al. (1983), tagged freshly-caught dead fish and placed them in the wells of fishing vessels at sea. They estimated that about 70 percent of the skipjack they tagged were returned by unloaders and cannery workers. However, tags attached to freshly-caught fish may be more easily knocked off and lost during loading and unloading than tags attached to fish which had been tagged and released weeks, months, or years previously.

3.2.5 Directed and Random Movements

Harden Jones (1968) recognized three types of "migratory movements": drifting with the currents, random locomotory movements, and oriented locomotory movements. In a later paper (Harden Jones 1984) he stated, "I use the word migration in the sense of coming and going with the seasons on a regular basis." Jones (1956 and 1966), using physical diffusion models, derived equations for calculating the directed (V) and random (A^2) components of the movements of a group of tagged fish, and Bayliff and Rothschild (1974) derived a crude method for adjusting the return data for uneven distribution of fishing effort. In the strictest sense, the movement is not random unless V is equal to zero, which has never been the case in any tuna study. The central issue is to determine why V is not equal to zero. Four explanations exist for apparent nonrandom movement, and each is discussed below.

First, if fish were tagged near a coastline the recapture data would probably show that fish had moved offshore and parallel to the coast in both directions and that the center of abundance of the recaptures was further offshore than the center of abundance of the releases. This does not indicate, except in the strictest sense, that the movement of the fish was non-random. In fact, the same pattern would result if dye molecules were injected near the edge of a barrier.

Second, the fish might encounter concentrations of food by moving randomly, and by random movement remain there until the food was nearly exhausted. This behavior would produce values of V greater than zero, but few investigators would classify this behavior as directed movement.

Third, fish are able to sense gradients in physical, chemical, and biological properties of the environment and follow such gradients to a richer food environment. In some cases these movements may be related to irregular environmental events and in others to such regular seasonal events as warming and cooling of the surface water in temperate regions. In the latter case the tuna could be orienting to navigational cues (gradients in the earth's magnetic field, or angle of a celestial body) rather than gradients in food abundance or other properties that determine the suitability of the habitat. According to the definition of Harden Jones (1984), such seasonal movements would be migrations, regardless of the mechanisms involved.

Fourth, some fish, such as bluefin and albacore, make spectacular seasonal movements, but the factors controlling these movements are much less well understood than such seasonal events as the movement of skipjack into temperate New Zealand waters in the spring and out of those waters in the fall. Homing, defined by Gerking (1953) as "the return to a place formerly occupied instead of going to other equally probable places", seems to be involved here.

Ideally, in the development of a model using tag recovery data one might first subtract such effects as proximity to land, then non-seasonal effects such as patchy distribution of food, and finally easily-understood seasonal effects such as poleward movement during the spring and the reverse during the fall. This would leave homing effects as the residual. Considerable interest exists in this subject, especially for skipjack in the Pacific Ocean (SPC 1981). Present data may not be adequate for such an analysis but some of the research approaches we propose in subsequent sections may make such an approach practical in the future.

In general, the ratio of V to A^2 would be expected to be greater for highly-migratory species, such as bluefin and albacore, than for species without evident well-defined movements. Unfortunately, no estimates of V or A^2 are available for bluefin or albacore, but such data for yellowfin and skipjack, from Bayliff (1984), are shown in Table 2. In every case the $(V \times 1000)/A^2$ value is greater for skipjack than for yellowfin, indicating that the movements of skipjack in the eastern Pacific are more directed than those of yellowfin.

3.2.6 Integrity of Schools

Skipjack do not appear to remain in the same schools for long periods of time. During the first 1 to 3 months after release fish tagged in the eastern Pacific Ocean at the same location on the same date are not randomly mixed with untagged fish in the same area, but by the fourth month random mixing has taken place (IATTC 1984: 33-36). Present evidence for south Pacific skipjack also indicates that schools do not maintain their integrity for long periods (Kleiber and Argue, MS); this evidence includes analyses of western Pacific data for instances of multiple recoveries of tagged skipjack from the same school recaptured on the same date, and

Table 2

Estimates of V and A^2 for yellowfin and skipjack (from Bayliff 1984).

Region	Year	Yellowfin V	Yellowfin A^2	Yellowfin $\frac{V \times 1000}{A^2}$	Skipjack V	Skipjack A^2	Skipjack $\frac{V \times 1000}{A^2}$
Colombia	1981	0.5	835	0.6	2.9	426	6.8
Gulf of Panama	1959	1.4	776	1.8	1.4	449	3.1
Gulf of Panama	1961	2.9	2065	1.4	2.8	1816	1.5
Gulf of Panama	1981	0.6	232	2.6	1.1	293	3.8
S. Central America	1979	0.8	2719	0.3	2.4	2678	0.9
S. Central America	1980	0.7	479	1.5	1.7	985	1.7
S. Central America	1981	1.9	2180	0.9	4.1	779	5.3
N. Central America	1979	2.3	3821	0.6	4.5	2406	1.9

studies of data for rare blood serum alleles. Analyses of this type have not been performed for other species, but anecdotal evidence suggests that the schools of other species of tunas do not retain their integrity for long periods.

3.2.7 Additional Mark and Recapture Studies

A large fraction of the data on marking and recapture in the files of various fishery agencies has not been fully analyzed. Analyses have not been completed in some cases because the investigations have only begun, but in others the work could be done if money and manpower were allocated. In addition, little tagging of tunas has been done in some regions, such as the Indian Ocean and Philippines-Indonesia region, and relatively few individuals of bigeye in the Pacific Ocean and *Euthynnus* spp. and *Auxis* spp. in any ocean have been tagged. Bigeye are of great commercial importance in the eastern Pacific Ocean, but as nearly all are caught with longline gear, large-scale tagging is impractical using present technology. (This is not the case in the Atlantic Ocean where bigeye tagging can be easily conducted.) *Euthynnus* and *Auxis* are currently of only minor commercial importance in most areas, but this is likely to change. Large-scale tagging of these two genera is presently impractical except in a few areas such as Japan, the Philippines, Senegal, and Indonesia, where they are relatively heavily exploited.

3.3 Tunas and Their Ocean Environment

3.3.1 Introduction

Oceanic environmental variables and processes that affect tunas vary spatially and temporally over a large array of time and space scales in three dimensions. Sette (1961) stressed that to understand and eventually model the effects of the ocean environment on fish populations, information on the "changing ocean" and on average ocean conditions is needed. The "changing ocean" is caused by variations of the interaction at the ocean surface between air and sea: wind stress, heat exchange, precipitation, evaporation, and advection.

Tunas differ in their environmental and habitat requirements and these requirements change over their life history. Yellowfin, skipjack and bigeye are restricted to tropical waters, whereas albacore and bluefin are found in temperate seas. Juvenile stages of skipjack and albacore live in shallower depths than adults and migrate more extensively.

The mechanisms that link the ocean environment to tuna movement are not well defined or understood. In some cases ocean conditions are believed to act directly on the biology of the tunas, while in other cases the relationship with ocean conditions is indirect through their forage. The distributional limits of various species may be set by specific oceanographic properties acting directly on the physiology and/or behavior of individuals in the population. For example, albacore apparently are not able to thermoregulate effectively at temperatures below about 10°C (Graham and Dickson 1981), and this may be why the species is usually not found in waters cooler than 10°C. Variations in the availability of tunas within their distributional limits may not be linked with ocean conditions acting directly on the tunas, but rather indirectly through the distribution and abundance of forage organisms. For example, the availability of tunas within their distributional range is usually greatest in the vicinity of oceanic fronts where food abundance is high (Uda 1973, Laurs and Lynn 1977, Laurs et al. 1984). To identify the optimal approach for studying this multivariate three-dimensional system is a major challenge. We discuss here the status of knowledge of the relationship between tuna movement and the environment and possible directions of future research.

3.3.2 **Limits**

A focus of much of the past work on tuna movements and distributions has been on physical characteristics of the habitat at the extremes of horizontal and vertical distributions of tunas. This work has been reviewed most recently by Sund et al. (1981) and documentation for much of the following can be found in their publication. Correlations, which have been well described in the literature, exist between tuna catches and the physical environmental barriers indicated by sea-surface temperatures, mixed layer depth, and oxygen concentration. The principal evidence of the effect of temperature on tuna distribution has been the seasonal expansion and contraction of the range of surface-caught fish at the periphery of their ranges and this expansion and contraction correspond fairly well to sea-surface isotherm displacements (Blackburn 1965; Champagnat and L'homme 1970; Cayré et al. 1974). In the same statistical sense temperature and possibly oxygen also establish vertical habitat limits for tunas. Such statistical evidence of the extremes of the potential habitat of tunas has proven to be quite useful for fishery operations, but much more detailed cause and effect relationships which would forecast movement are lacking.

In the past, the thermocline was thought to represent a limit to vertical distribution of tunas. This relationship is in part based on work relating purse seine fishing success with thermocline depth (Green 1967). Also, skipjack occur in many areas of tropical seas where they are not available to surface gear (Sharp 1978), their presence being indicated by their larvae (Nishikawa et al. 1985) and by anecdotal evidence of bird flocks feeding on forage driven to the surface by feeding fish. Such observations have led some to believe that this subsurface existence provides a refuge from surface fishing gear. Recent results from tuna tracking studies show that tuna spend much of their time within the thermocline (Yonemori 1982; Laurs and Dotson, in prep.) and suggest that tuna are "creatures of the thermocline". In fact, the thermocline may not act as a barrier, but rather determine the degree of vulnerability of tunas to surface and subsurface fishing gear. When the thermocline is shallow the fish are more vulnerable to surface fishing gear and vice versa. Also, longline fishing successs is markedly higher when hooks are set in the thermocline rather than at depths above it (Laurs and Dotson, MS).

The concept of limits in the distribution of tunas is indicated in acoustic tracking studies which were conducted to investigate the vertical distribution of tunas, although this concept has not been strongly supported by laboratory work (Matsumoto et al. 1984). Laboratory work indicates that kawakawa (Euthynnus affinis) penetrate oxygen or thermal barriers for a food award, and these barriers are far more extreme than fishery correlates would predict (Matsumoto et al. 1984). Lethal limits exist in the ocean; in the central North Pacific (Figure 12) at 11°N lat., oxygen concentrations of only 0.5 ml/l occur within 100 m of the surface. Partial pressures of oxygen below 50% of saturation or temperatures below 10°C are lethal for albacore (Graham and Laurs 1982; Graham and Dickson 1981). Lethal limits are probably seldom significant in the mortality of tunas as the fish would retreat before they became lethal. Some anecdotal evidence indicates that direct effects of temperature might occasionally be the final cause of death. Tracking studies indicate that injured tuna, swimming too slowly to maintain hydrostatic equilibrium, slowly glide into colder water which causes them to swim even slower, increasing their rate of descent into ultimately fatal conditions. Perhaps this is the manner in which starving tuna die. Future work should emphasize using the high technology of acoustic tracking and archival tagging along with concurrent measurements of the ocean using observations made from ships and satellites. Data resulting from these types of studies should aid understanding of the oceanic limits and habitats of tuna.

3.3.3 Forage

Striking differences exist in tag recovery rates or in CPUE between regions and seasons suggesting differences in local concentration or vulnerability of tuna to the fishery or both. Dramatic variations in catch rates are common in tunas, indicating the crucial role of the environment in concentrating tunas and affecting their availability to surface fisheries. Future investigations, therefore, must be concerned with discovering the "crucial" environmental mechanisms.

When aggregations of tunas occur near the surface along edges of oceanic provinces and other oceanic fronts, usual explanations are that tuna forage is more abundant or more available in such localities or that the sharp thermal or salinity gradients constitute physiological barriers to tuna movement. The latter argument has not been supported by the experimental findings. On the other hand, the well known correspondence between tuna catch and ocean productivity, illustrated in Figures 13a and 13b (for Atlantic tuna fisheries), indicates that such aggregations are related to the availability of forage. Forage abundance or availability becomes the crucial environmental variable for explaining the abundance of tunas in such areas (Stretta et al. 1975), yet no adequate quantitative assessments of the abundance of forage exist. It seems essential that forage or a reliable index of it be measured in such areas to confirm this hypothesis. Such indices should account for the vertical migrations of mesopelagic organisms (King and Iverson 1962) as well as epipelagic organisms. Acoustic methods and midwater trawls seem promising in this regard. In addition to direct measurement of forage, a reliable and easily measurable index of forage abundance is needed.

Prediction of forage abundance may depend on identification of the appropriate time lag between the onset of a productivity event and tuna catches. The time lags vary with region, times of year and other variables. For example, different scenarios exist for the different

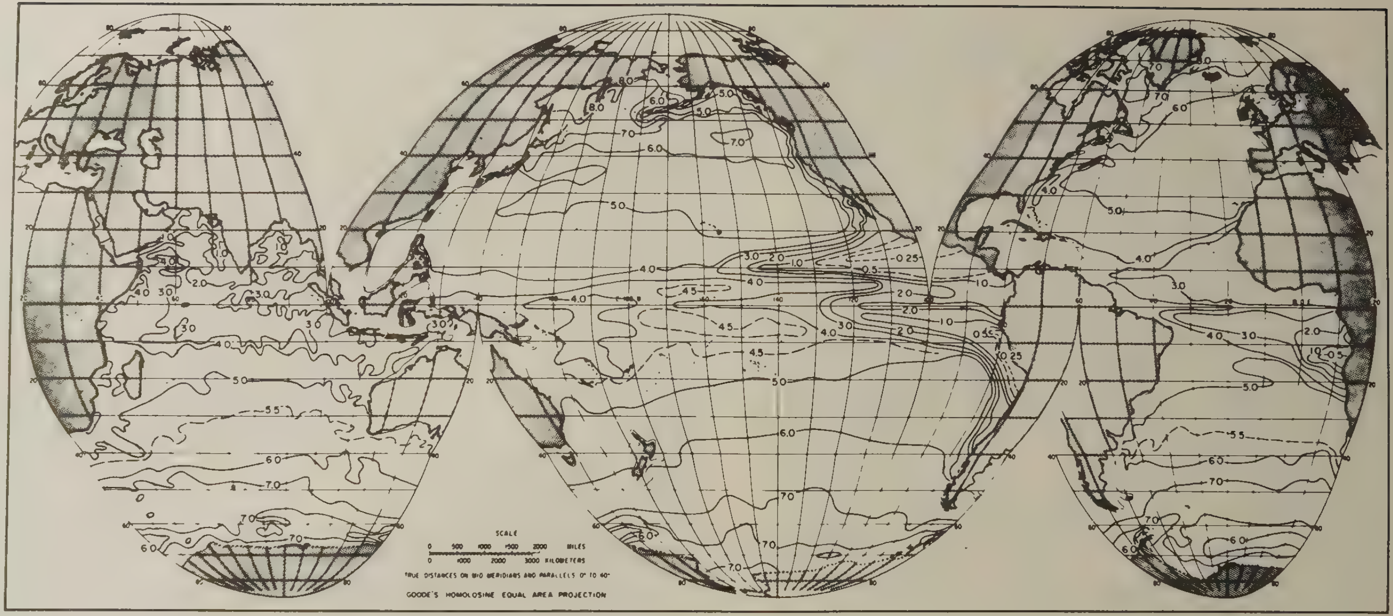

SCALE
0 500 1000 1500 2000 MILES
0 1000 2000 3000 KILOMETERS
TRUE DISTANCES ON MID MERIDIANS AND PARALLELS 0° TO 40°
GOODE'S HOMOLOSINE EQUAL AREA PROJECTION

Figure 12. Distribution of dissolved oxygen (ml/l) at 100 m in the world ocean (from Reid et al. 1978).

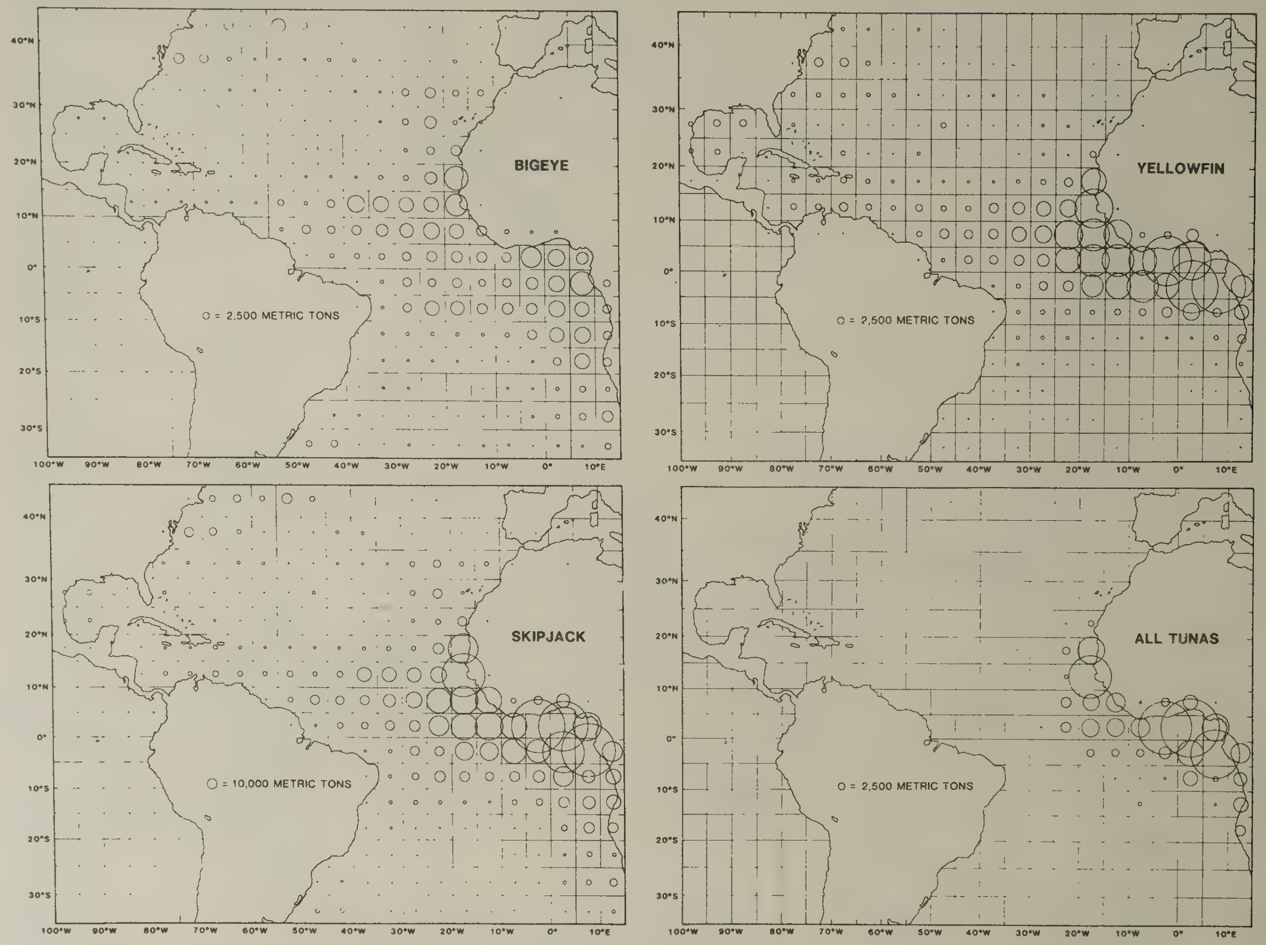

BIGEYE
O = 2,500 METRIC TONS
YELLOWFIN
O = 2,500 METRIC TONS
SKIPJACK
O = 10,000 METRIC TONS
ALL TUNAS
O = 2,500 METRIC TONS
40°N
30°N
20°N
10°N
0°
10°S
20°S
30°S
100°W
90°W
80°W
70°W
60°W
50°W
40°W
30°W
20°W
10°W
0°
10°E

Figure 13a. Average catch of bigeye, yellowfin, skipjack tuna, and all tuna summed by 5° areas. The area of a circle is proportional to catch (prepared from ICCAT data base).

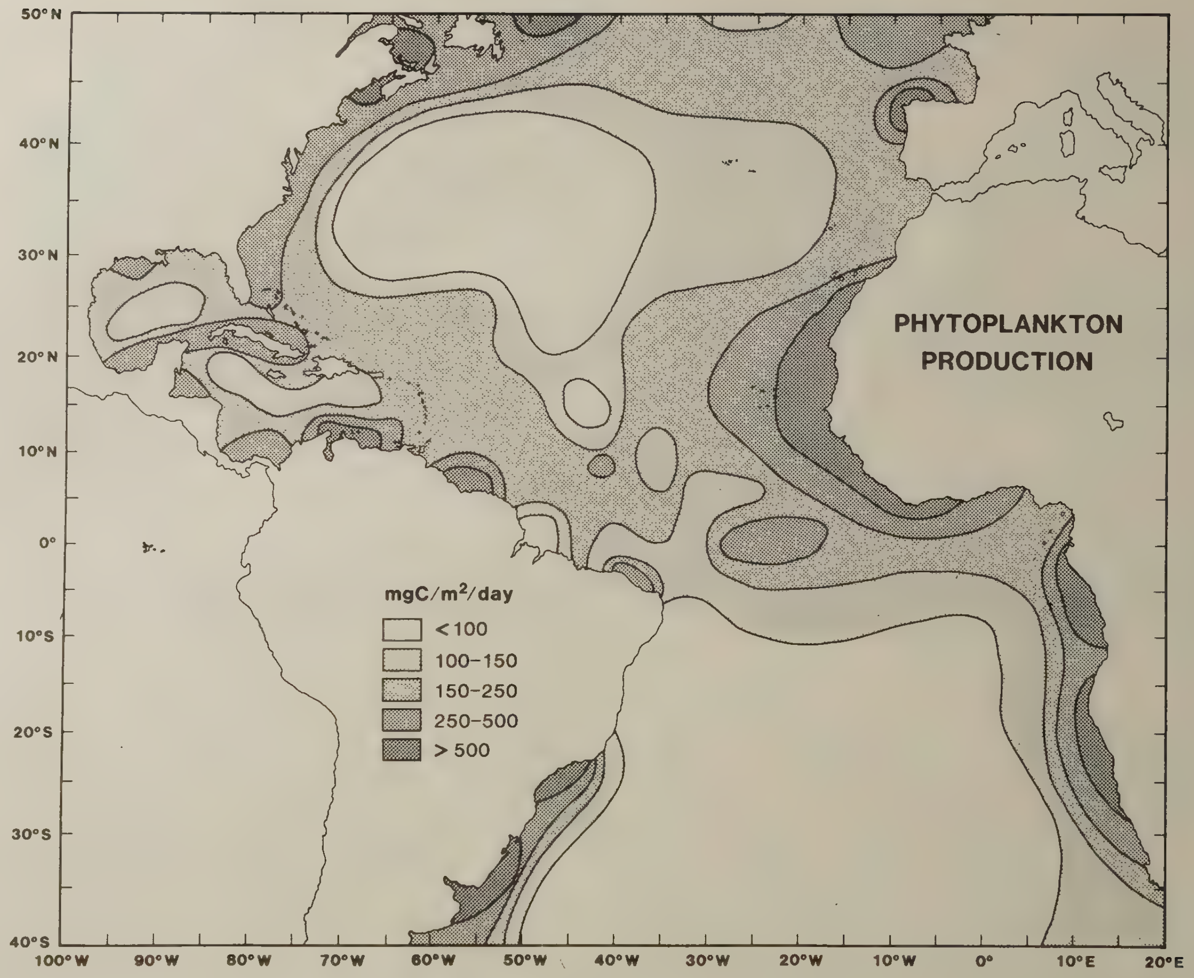

PHYTOPLANKTON
PRODUCTION
mgC/m²/day
< 100
100–150
150–250
250–500
> 500
50°N
40°N
30°N
20°N
10°N
0°
10°S
20°S
30°S
40°S
100°W
90°W
80°W
70°W
60°W
50°W
40°W
30°W
20°W
10°W
0°
10°E
20°E

Figure 13b. Average phytoplankton production (after Koblentz-Mishke et al. 1970; FAO 1972).

frontal areas in the eastern Atlantic; each region of the African coast shows a somewhat different rate of development (J.-M. Stretta, unpublished data). The onset of a typical event (rising of nutrients into the euphotic zone) occurs 4-6 weeks prior to the development of a fishery in the region (J.-M. Stretta, unpublished data).

3.3.4 Processes

Wind-driven advection and mixing are principal physical processes that determine forage production and distribution. On the largest scales, zones of convergent and divergent flow occur consistently.

Divergent zones are biologically productive because nutrients are brought vertically to the euphotic layer, but organisms are dispersed laterally. Proximate convergent zones can collect this production. On somewhat smaller scales of time and space, wind-driven convergent and divergent flow along coastlines creates special environments for tuna and forage. Usually tunas avoid upwelling (divergent) zones but frequent the downwelling (convergent) fronts usually found seaward of upwelling sources. This is presumably due to the higher forage associated with such fronts. Convergent fronts also are produced where colder or more saline water meets warmer or less saline water. At 3-5°N, cold water from the equatorial upwelling meets warm countercurrent water and slides downward. The process is expressed as a series of thermal fronts encountered in this region, especially in the eastern half of the Pacific Ocean basin. River plumes, such as those of the Columbia and Amazon Rivers, have frontal zones due to lateral impingement of saline waters on fresher water of the plume.

The converging effect of the wind stress distribution causes the thermocline to deepen (usually called downwelling) and tends to have low productivity. Examples are the central areas of the large ocean gyres where the thermocline is deep and the water is highly transparent. Temperature and/or salinity fronts are found around the periphery of these central areas. For example, in the Hawaiian region a salinity front moves seasonally north-southward into the island region. Associated with this frontal movement is the seasonal movement of skipjack into range of the local fishery (Seckel 1972). Similarly, high catches of skipjack in the western Pacific seem to be correlated with the 35 $^{o}/oo$ isohaline. Presumably the higher catches are due to aggregation of skipjack on forage produced in convergence zones which are marked at the surface by the 35 $^{o}/oo$ isohaline (Donguy et al. 1978).

Eddy motions also create convergent or divergent flow, depending on flow direction and Coriolis deflection. Cyclonic eddies produce divergent flow and tend to produce higher production in their centers, such as the Costa Rican Dome. Recent evidence (Tranter et al. 1983) indicates that biotic enrichment can occur at edges of anticyclonic eddies. Demonstrably different organism ensembles occur in eddies of both types (Wiebe et al. 1976; Backus et al. 1969).

On a smaller scale, fronts or convergences can also be produced by the interaction of the wind-driven surface flow with ocean currents, or they can be the result of eddying water motion. In all cases forage organisms are redistributed, diverged or converged by these water movements.

3.3.5 Fronts and Visibility

In the albacore fishing grounds at the border of the North Pacific Ocean, the fish concentrate in the vicinity of ocean fronts. These fronts are associated with: current systems and other features in the western Pacific (Uda 1973); coastal upwelling (Laurs et al. 1977; Laurs et al. 1984); and the Columbia River plume in the eastern Pacific (Owen 1968;

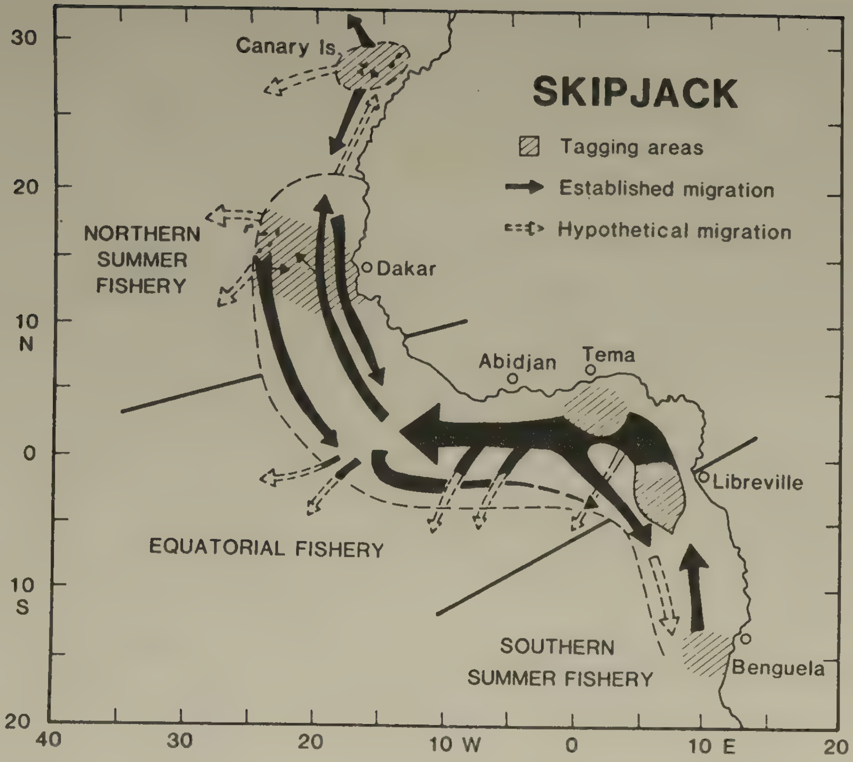
Pearcy and Mueller 1970). The migration patterns and fishing success for albacore in the central North Pacific are also related to oceanic frontal structure associated with the North Pacific Transition Zone (Laurs and Lynn 1977 and Lynn 1984). Similarly, skipjack and yellowfin do not enter the green water of coastal upwelling areas in the Gulf of Guinea and the Gulf of Panama but remain in the clear oceanic water along the edge of the front. In addition, phytoplankton stocks and production are highest on the Costa Rican Dome (about 9°N, 89°W), while zooplankton is more abundant and tuna catch highest along the edges (F. Miller, unpublished data, IATTC, La Jolla, CA, USA).

This pattern in the distribution of tunas along coastal fronts has led to the hypothesis that tunas do not enter the more turbid coastal waters because lower visibility reduces foraging efficiency; they remain along the edges of such habitats where the visibility remains high and capture prey from the coastal habitat as they stray into clearer water. An alternative explanation is that prey become concentrated in the front and are therefore more abundant than in either the coastal upwelled water or the offshore water. We believe sufficient data exist on the vision of fishes and underwater visibility to develop an optimal foraging model to test the visibility hypothesis.

3.3.6 Movements

Some evidence exists that variations in oceanographic conditions affect the timing of the onset of migration of albacore from one part of the North Pacific to another, and affect the rates of migration and routes that the fish follow during migrations. For example, the timing of the emigration of fish in the western North Pacific appears to be determined by conditions associated with the Kuroshio Current system (R.M. Laurs pers. comm.). Emigration from the eastern Pacific is not understood, nor have its relationships with ocean conditions been defined, except in general terms of seasonal cooling of the ocean (Flittner 1968). The routes followed by albacore on their migrations across the North Pacific are believed to be associated with the Transition Zone (McGary et al. 1961) and mid-ocean frontal structure (Laurs and Lynn 1977). The migration rates and aggregations of albacore in the mid-ocean are markedly influenced by the degree of frontal structure development (Laurs and Lynn 1977). Variation in oceanographic conditions might have similar effects on the well-defined spawning migrations of Atlantic and Pacific northern bluefin.

Much less is known of the migrations of skipjack and yellowfin, and even less is known of the effect of variation of oceanic conditions on their migratory patterns. In fact, some stocks appear to be more nomadic than migratory. In the eastern Atlantic skipjack follow a predictable route, apparently moving from one area of high productivity to another along the African coast (ICCAT 1984 ; Figure 14). They then seem to disappear from the coastal fishery, probably moving offshore along the equator. However, the seasonal movements may be more related to changes in forage availability than to an inherent migrational cycle. In contrast, the extensive tagging work on the South Pacific skipjack indicated no consistent patterns of movement, although fisheries in the region show a seasonal pattern. Broad trends must exist but they could not be resolved due to seasonal movement of the tagging vessel (Lewis 1981; Argue and Kearney 1982). The short-term (30 days or less) recoveries of skipjack indicated only dispersion, whereas over longer periods the tagging data show somewhat more directional consistency (A.W. Argue, unpublished data). As before, this indicates that the scale of movement is a critical consideration in studies of movements. Movements considered on a monthly basis may appear random, but with longer periods, patterns may emerge showing a net directional component. In other words, a fixed geographic coordinate system may be inappropriate for tuna, since a fish can follow the same inherent rules in such a system without following the same path.


SKIPJACK
▨ Tagging areas
Established migration
Hypothetical migration
Canary Is.
Dakar
Abidjan
Tema
Libreville
Benguela
NORTHERN SUMMER FISHERY
EQUATORIAL FISHERY
SOUTHERN SUMMER FISHERY
30
20
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0
10 S
20
40
30
20
10 W
0
10 E
20

Figure 14. Migration pattern for skipjack tuna in the eastern Atlantic from International Skipjack Year Program tagging experiments (ICCAT 1984). Solid arrows depict observed movement of fish from tagging areas. Open arrows depict possible movements, not yet confirmed by tagging.

Other boundaries exist in the ocean that could be used as coordinates relative to which tuna distributions could be described. Moving frontal zones with which the tuna are associated is one such example.

Water motion affects fish during migration, but passive or selective transport (Arnold and Cook 1984) by currents has yet to be identified as the mechanism used by tuna in any of their migratory routes, although a number of such mechanisms have been postulated. Examples include the transport of skipjack young to the eastern tropical Pacific (Seckel 1972; Williams 1972), and movement of southern bluefin to their spawning grounds in the South Pacific and transport of their juveniles to Australian waters (Harden Jones 1984). The dispersive element in the short-term recoveries of marked skipjack and other tunas might also be related to water movements. If the fish were foraging in a limited area, they could be dispersed by the eddy motion of the water. The effects of water motion should be included in all studies of tuna movement or migration until it can be demonstrated that they are negligible.

The regular transoceanic movements of the temperate tunas suggest that tuna have the ability to navigate. Walker et al. (1984) have postulated a possible compass and piloting mechanism. In addition, yellowfin tagged off

Hawaii return to fish attraction devices on a regular basis and at about the same time of day (Holland et al. in press). The inherent navigational component of movements is not a key management issue in most tuna stocks because if it exists it is equivalent to the known average pattern. What we need to know is how to predict the anomalies from the average pattern. On the other hand, if a channeling of movements existed as a result of navigation cues, or transport by currents, it could have direct management implications.

3.3.7 Opportunities for Cooperative Studies

Major new initiatives in oceanography have started and are planned for the remainder of this century. These initiatives will provide new understanding of ocean structures and processes and provide opportunities for interdisciplinary studies. The Tropical Oceans, Global Atmosphere (TOGA) international program began in 1985. This program will lead directly into the World Ocean Circulation Experiment (WOCE) which is scheduled to begin in 1990. The first is particularly pertinent to studies related to tropical tunas. The latter program will make use of vast arrays of observations including those obtained from new satellite sensors measuring wind stress and sea level. It is probable that, when the programs are completed, the variability of the equatorial current systems and the thermocline depth can be modeled and predicted. As a result, more detailed information about ocean structure, ocean currents, frontal developments and distributions will become available.

Drifting buoys that can be tracked by satellites provide a new opportunity to study tuna movements as they are related to currents. The buoys could be deployed during a tagging cruise and the dispersive element of the water as reflected by both surface and subsurface buoys could be compared to the apparent dispersion of fish indicated from short-term or longer-term recoveries of tags. This experiment would test the hypothesis that variation in the headings or dispersion of short-term recoveries of marked tuna is related to transport by currents. This approach could be integrated with the TOGA program since, as part of TOGA, an extensive expendable bathythermograph observational program is in progress. Information, so far unavailable, will be obtained about the subsurface temperature structure and its month-to-month changes in the tropical Atlantic and Pacific.

In short, a wealth of environmental data will soon be available for the study of tuna movement dynamics. The data can be used to test hypotheses regarding movements using existing movement data. In addition, the programs provide a data field around which international sea experiments on tuna movements could be designed. Physical oceanographers are receptive to making their studies interdisciplinary, and funding agencies favor cooperative work. Cooperation must be sought with the oceanographers and their funding agencies to establish such an interdisciplinary program. Steps should be taken to combine fishery research objectives with those of international oceanography and to ensure that the wealth of incoming oceanographic data will be in a form useful for interpreting tuna movements. However, more data on actual paths of tunas must be obtained before any major advances can be expected in the dynamics of tuna movements, or before the wealth of environmental data can be fully utilized in the interpretations of movements.

3.3.8 Research Approaches

We need to forecast from physical data where tunas will be, their numbers, and their vulnerability to fishing gear. If their food distribution can be described and predicted or if habitats which are more likely to be selected by tunas can be described and predicted, then the distribution of tunas could be described and predicted. Thus, a model is added that describes the process of movements and then forecasts movements on the basis of the driving variables. Such a model would have great value where the fishery is composed of a mosaic of national jurisdictions. A model similar to this is being developed for North Pacific albacore (P. Kleiber pers. comm).

Powerful statistical techniques have recently been employed to identify tuna-environment relationships in the eastern tropical Atlantic (Mendelssohn and Roy 1986). These techniques involve multivariate, time series models that use temporal and spatial distributions of tuna, catch rates, and environmental properties such as sea-surface temperatures, mixed layer or thermocline depths, and wind stress. These models identify significant environmental properties, show phase relationships in cyclical fisheries, and identify lags between oceanographic events and increased catches. This type of model is most easily applied when obvious correlations exist between environmental conditions and catch, but the processes are not identified.

Research planning must consider whether funds should be expended to understand relationships between environment and movements or identify correlations. In the past, management needs seemed satisfied by the latter approach, but no consensus exists among experts on the preferred approach. One view was that it was preferable to link tuna movements to the environment by establishing cause and effect relationships, because past correlations have ultimately broken down. The alternative view was that such linkages were difficult to establish and difficult to apply to real fishery problems and that the proper approach was to become more sophisticated in measurement of the environment and tuna movements; then the correlations would hold. The latter view supports large-scale measurements and broad project objectives, whereas the former view would lead to a series of smaller-scale and highly focused investigations designed to test specific hypotheses. Examples are testing how movement rates vary with forage patterns and physiological state or how visibility affects foraging patterns. Extensive use of ocean measurements made by satellite should be most beneficial in such work.

The development of a major program on movement dynamics of tunas must address the issue of scales. Most management issues are large scale (5,000-10,000 km), whereas the events that affect movement on a daily basis are of smaller scale (50 km). The approaches to integrate these fundamental differences in scale will be a key issue in the development of a program on tuna movements.

3.4 Reexamination of Tuna Movement Data

This section addresses the importance of reexamining existing data as a prelude to developing a major research program on tuna movement. Much information on movement has been collected in the last 30 years for the six principal tuna species (skipjack, yellowfin, albacore, bigeye, northern bluefin, and southern bluefin). The primary data include conventional tag and recovery data and catch and effort data; secondary data include oceanographic and climatic data, data pertaining to stock identification, size and age of the catch, diet, reproduction and general ecology and biology of adults and juveniles. The approximate numbers of tag releases for each species in the world's oceans (Pacific, Atlantic and Indian Oceans) is roughly proportional to the distribution of current world catch (Tables 3 and 4).

Table 3

Approximate numbers of tag releases for the principal tuna species (from Bayliff, Fonteneau, and Kearney, pers. comm.).

Ocean:	Atlantic	Indian	Pacific	Total
Skipjack	35,000	0	280,000	315,000
Yellowfin	14,000	0	140,000	154,000
Albacore	6,000	0	25,000	31,000
Bigeye	8,000	0	1,000	9,000
Northern bluefin	23,000	0	15,000	38,000
Southern bluefin	-	0	60,000	60,000
Total	86,000	0	521,000	607,000
Percent	14.2	0	85.8	100.0

Table 4

The 1979 world catch in metric tons of the principal tuna species (from Joseph 1983).

Ocean:	Atlantic	Indian	Pacific	Total
Skipjack	87,714	32,662	578,309	698,685
Yellowfin	144,159	60,649	379,222	584,309
Albacore	74,325	12,233	114,696	201,254
Bigeye	33,060	31,632	121,684	186,376
Northern bluefin	13,330	-	20,108	33,438
Southern bluefin	7,629	18,142	7,109	32,880
Total	360,217	155,318	1,221,128	1,736,663
Percent	20.7	8.9	70.3	100.0

New lines of research could be explored through further analyses of existing tag recovery, catch-effort, oceanographic, climatic and other data. Investigators could attempt the following: identification of hydrographic and climatic features that have the greatest impact on movement and concentration of tunas; examination of seasonality in fisheries as it relates to movements of tuna (from catch-effort and tag recovery data); examination of directionality of tuna movements and of interaction among tuna fisheries (cooperative examination of tag recovery and catch-effort data); analysis of tag recoveries in relation to the size (age) of tuna in the fishery at the time the tags were recovered; cooperative examination of tag recapture data, oceanographic data and data on forage items (from diet samples), which might be indicative of tuna movement among ocean domains; and comparative studies of species and stocks.

With further analysis of existing data, the research proposed in this report could be refined, as could development of specific research hypotheses. On the other hand, without combining data from various regions and international and national agencies, exploration of existing data could prove misleading. For example, when blood electrophoretic data for Pacific skipjack included only those samples collected by the United States and Japan (Figure 15), it was hypothesized that skipjack in the Pacific comprised several subpopulations (stocks). When samples collected by the South Pacific Commission were included (Figure 16), it was concluded that clinal population structure was a reasonable alternative hypothesis. Tag and recovery data provide an example of how examination of large data sets can change conceptual models. If one examined only skipjack tag and recovery data collected by Japan in the central and western Pacific (Figure 17, upper), one would define the extent of skipjack movement much differently than if one had also examined the South Pacific Commission data (Figure 17, lower) and the Inter-American Tropical Tuna Commission data (Figure 18, upper). In Figure 18 (lower), which combines the long-distance movements from all three data sets, it can be seen that there is exchange of skipjack among each of the study areas although only a limited portion of the stock may make such extensive movements.

To a large extent tagging data cannot be analyzed without catch and effort data. Such data are usually confidential when used at the level of an individual vessel, but need not be so when vessels or vessel trips are not identifiable. To make the proper interpretations of results from integrated analysis of movement and fishery data one must have considerable experience with the fisheries. The same could be said of the integrated analysis of movement and oceanographic data. Agencies such as ICCAT are at an advantage in this regard because they maintain data bases on tagging and fishery statistics for several countries in an area that covers the range of most stocks of Atlantic tunas. The scientists associated with ICCAT thus have the benefit of a) complete sets of data, and b) the experience necessary to analyse the data. Similar regional systems are being established in the Indian Ocean by the Indo-Pacific Tuna Development and Management Programme (IPTP) and in the Western Pacific Ocean.

Clearly the benefits of a coordinated analysis of existing data are substantial. An important first step in development of an international research program on tuna movement would be to make available historic tagging data for analysis with fishery and oceanographic data. Cooperative analysis of these data could yield relationships not previously identified that in turn would affect structure and cost of a new research program.

3.5 Ultrasonic Telemetry

Deployment of ultrasonic transmitters on free-ranging tunas has provided nearly all present information on smaller-scale, horizontal and vertical movements. Investigators have followed tunas so equipped for up to 8 days, successfully tracking skipjack, yellowfin, bigeye, northern bluefin and albacore. A successful track--that is, a reported track--usually lasts over 5 hours, as shorter ones generally are not reported.

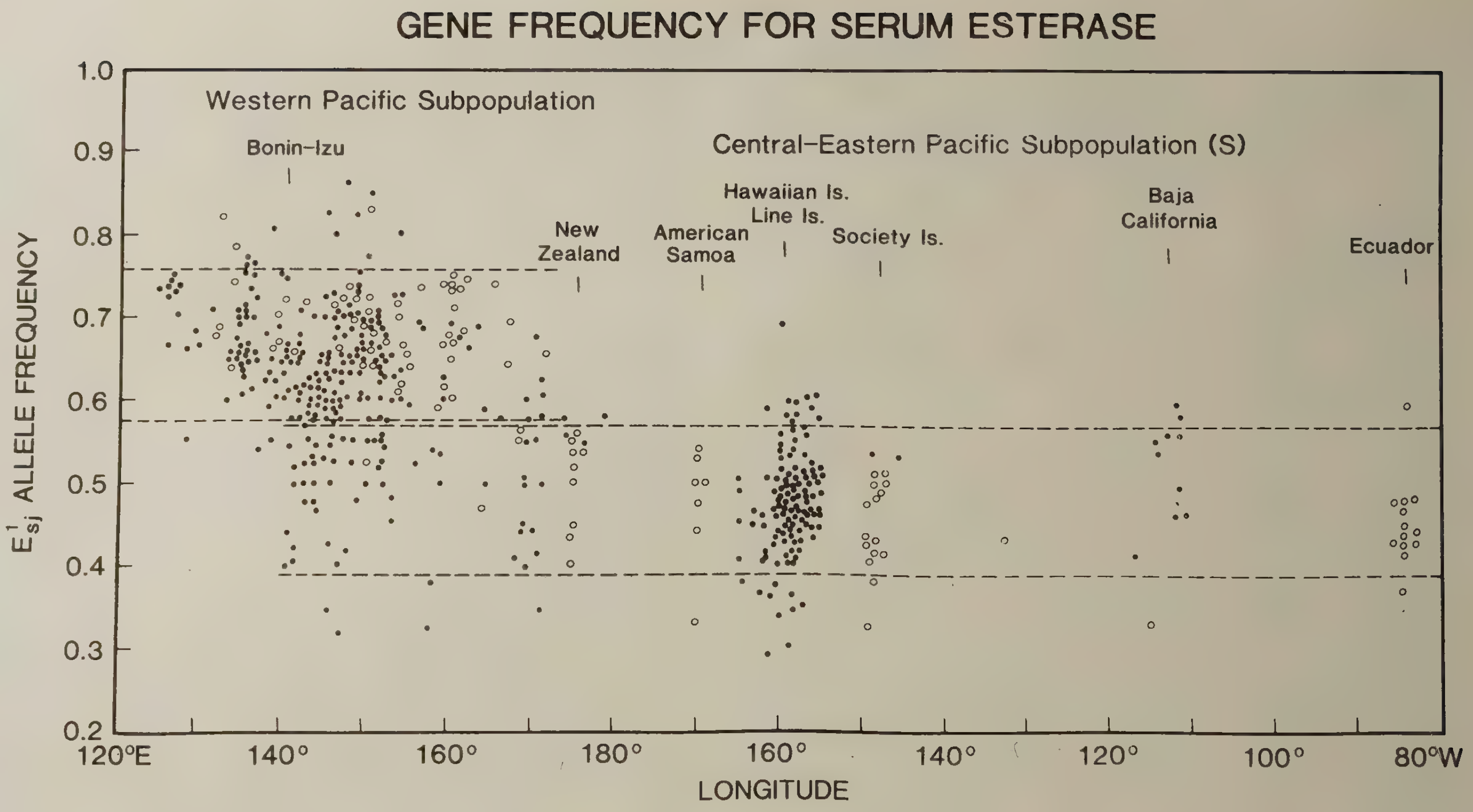


Figure 15. Gene frequency for serum esterase allele E^1_{sj} vs longitude of the sample location in the Pacific Ocean (from Fujino et al. 1981). Small dots and open circles represent individual lots of samples taken from the northern and southern hemispheres respectively. The dashed lines represent the 95% confidence limits of the "Western Pacific Subpopulation" (upper) and the "Central-eastern Pacific Subpopulation" (lower).

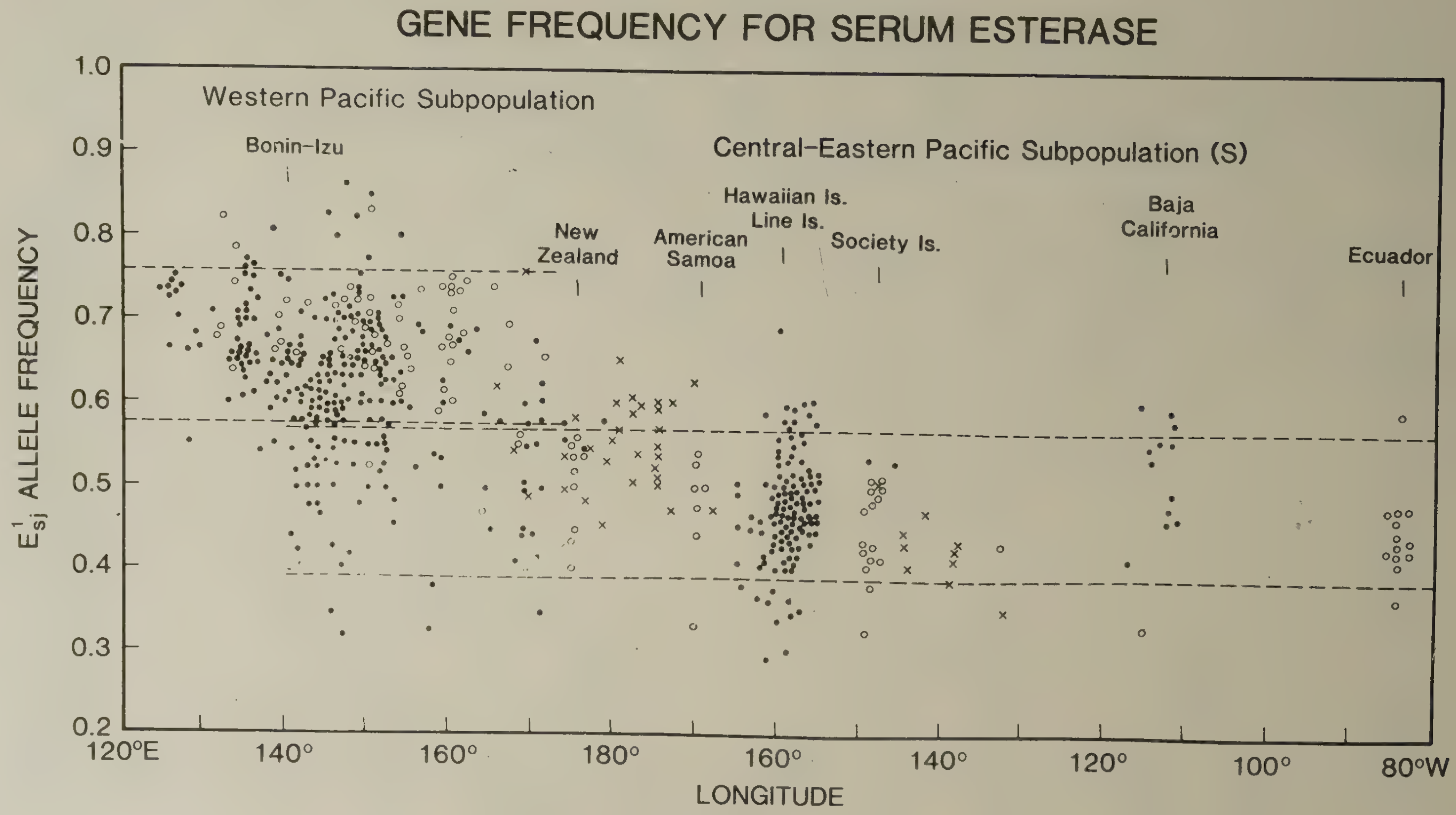
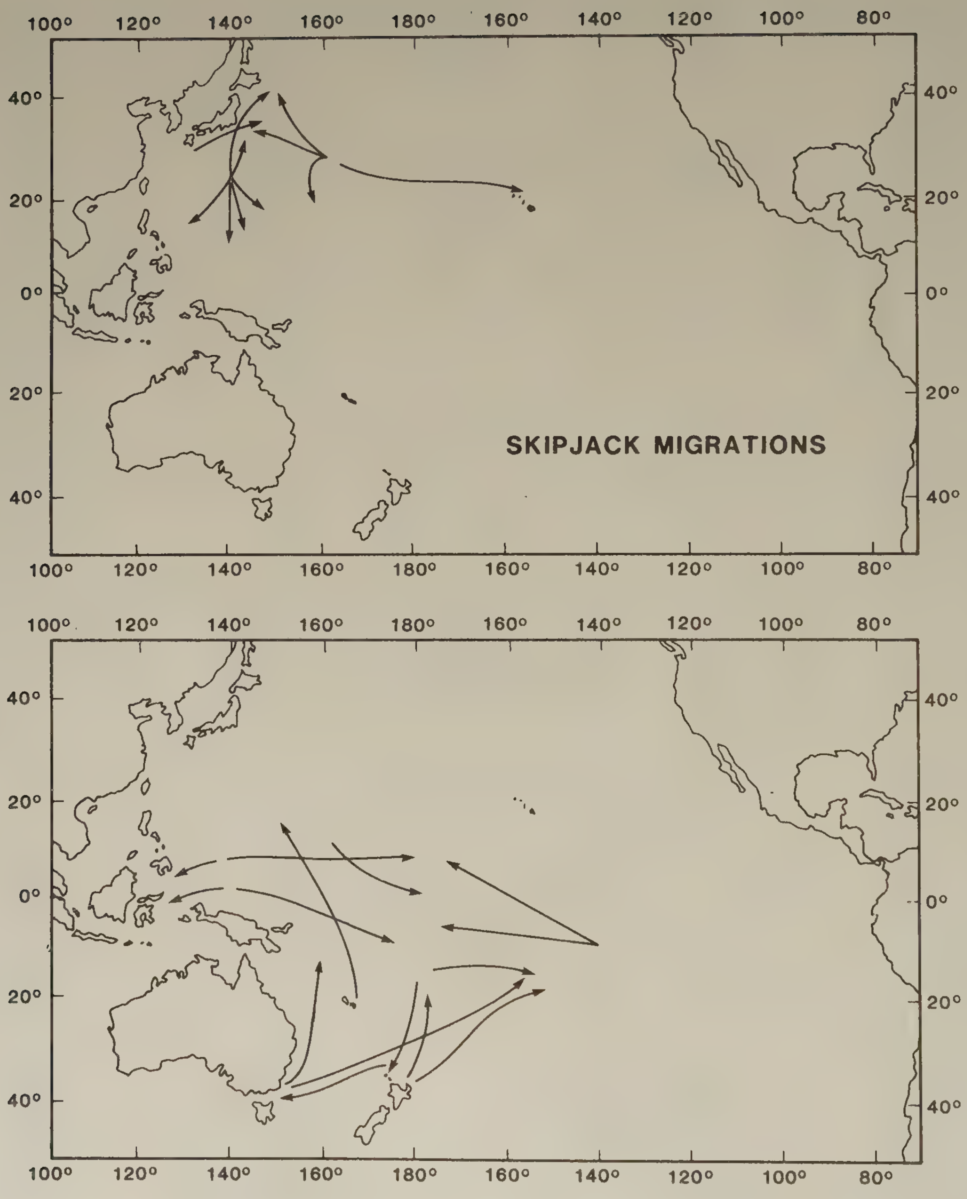


Figure 16. Gene frequency for serum esterase allele E^1_{sj} vs longitude of the sample location in the Ocean (from Fujino et al. 1981). Small dots and open circles represent individual lots of samples taken from the northern and southern hemispheres respectively. The crosses are South Pacific Commission samples (SPC 1981). The dashed lines represent the 95% confidence limits of the "Western Pacific Subpopulation" (upper) and the "Central-eastern Pacific Subpopulation" (lower).


SKIPJACK MIGRATIONS
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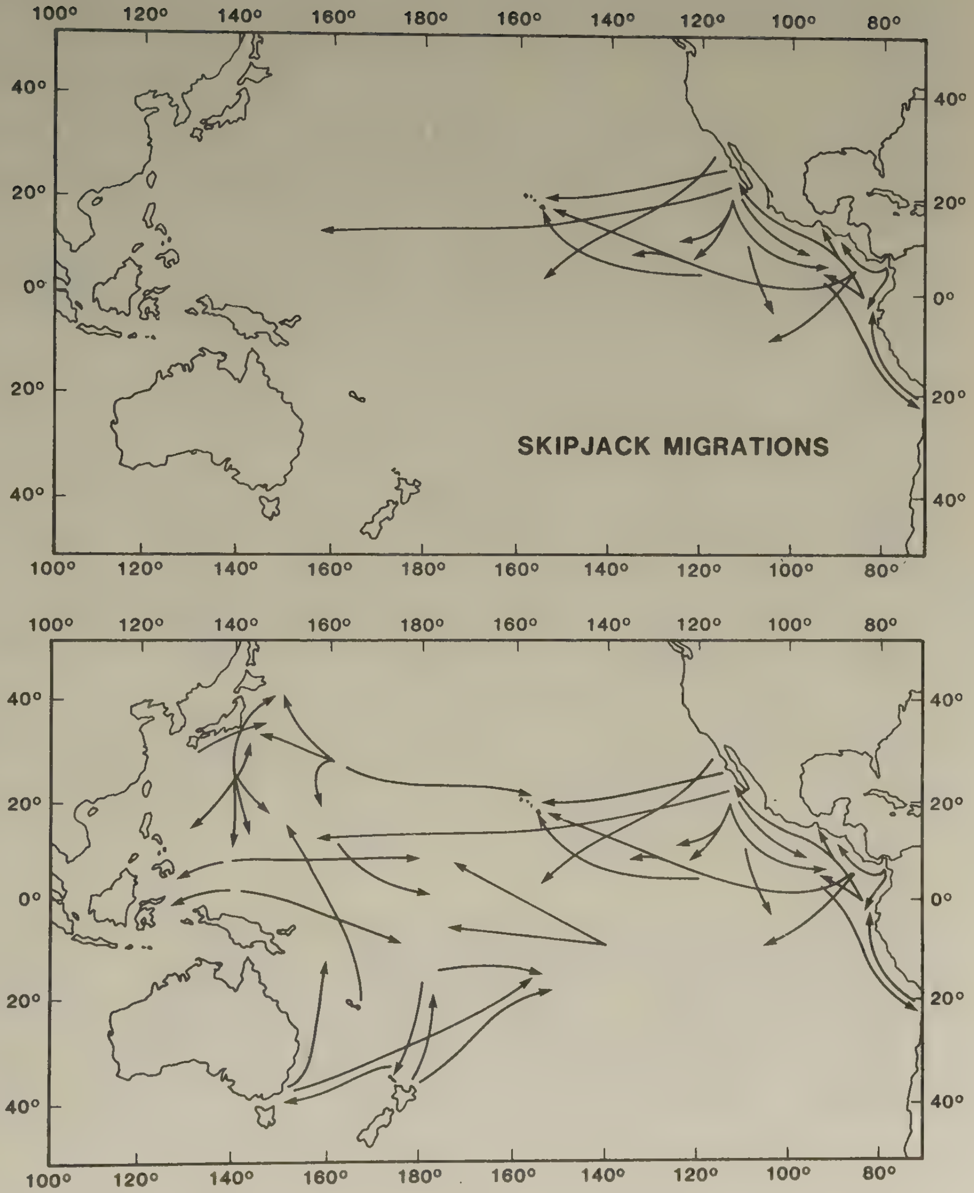
20°
40°

Figure 17. Upper; some long-distance migrations which have been recorded for tagged skipjack released by Japan in the Pacific Ocean (after IATTC 1984). Lower; some long-distance migrations which have been recorded for tagged skipjack released by the South Pacific Commission in the Pacific Ocean (after IATTC 1984; SPC 1984).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SKIPJACK MIGRATIONS

Figure 18. Upper; some long-distance migrations which have been recorded for tagged skipjack released by the Inter-American Tropical Tuna Commission in the Pacific Ocean (after IATTC 1984). Lower; some long-distance migrations which have been recorded for tagged skipjack in the Pacific Ocean (from IATTC 1984; SPC 1984).

While the fish is followed, data are collected that identify the horizontal path of the fish. If the transmitter is temperature- or depth-sensitive, data may also be collected on vertical excursions, temperature and depth distributions, swimming speed and associated oceanographic and biological correlates. Data on vertical position or water temperature have been collected at less than one-minute intervals, providing a highly detailed picture of the vertical excursions of free-ranging tuna. The only comparable data are some early observations using cine films of surface-feeding tunas taken from observation chambers of research vessels (Strasburg and Yuen 1960; Yuen 1966) or using sonar (Nishimura 1963; Yuen 1971).

In the following sections we outline typical tracking techniques, summarize the existing tracking data, identify some uncertainties, suggest a few management uses of ultrasonic tracking and draw three major conclusions from the existing tuna tracking information.

3.5.1 Tracking Techniques

(1) The Transmitter

Typically, the basic tracking system consists of a temperature- or depth-sensitive transmitter secured to the fish which is detected by directional hydrophone and receiver system located on the ship. The bearing of the fish, relative to the vessel, is determined by signal amplitude. The swimming depth or water temperature around the fish is telemetered by alterations in the pulsed repetition rate of the carrier frequency. The more rapid the pulse rate, the shallower the depth or the warmer the temperature.

Three major design criteria exist for a telemetry tag: size, life, and range. They are mutually exclusive because small size means small batteries and high resonant frequencies, which in turn limit life and range. If battery size is held constant, life is sacrificed for range or vice versa. Range, size and life are, in turn, determined by the source level or power of the transmitter, the carrier frequency, the pulse rate and length of the temperature- or depth-telemetering functions, and the size of the battery (Priede 1986).

To gain the maximum range from the minimum power input, the lowest possible carrier frequency should be employed. However, the resonant frequency of the signal generating element, the piezo-ceramic transducer, is inversely related to its size. Since the transducers are usually hollow cylinders, the largest tag diameter allowable for a particular application determines the minimum frequency. For tuna 40-80 cm long, 35 or 50 khz is usually employed in a tag of about 1.6 cm in diameter. For these frequencies a range of about 1 km under average tracking conditions is considered normal.

(2) Attachment of the Transmitter

In earlier tracking studies, the tag was forced into the stomach of tuna; when water temperature was monitored, a lead was run from the tag, through the opercular slit, to a thermistor exposed to the surrounding water. While having the advantage of rapid application and minimum trauma, two disadvantages readily became apparent. First, if the tag was large relative to the stomach volume, the tag was regurgitated, usually within hours. Second, the signal seemed significantly weakened by the fish's body (Laurs et al. 1977). As a result, in most recent studies tags are attached externallly using sutures or nylon "tie-wraps". The tag is placed either distal to the second dorsal or the anal fin or, in the case of bluefin (Carey and Lawson 1973), harpooned to the dorsal surface adjacent to the first dorsal fin. Wobbling of the tag, which causes erosion of the skin and underlying muscle, is eliminated by suturing at the front and midline of the tag (Holland et al. in press).

(3) **Tracking Procedures**

Tracking procedures are described by Holland et al. (in press), and will not be discussed in detail here. For successful tracking it is essential that the hydrophone be shielded from the water stream and securely mounted. It is important that the signal can be received while the boat is underway at a fairly brisk speed (approximately 6 knots). Holland et al. (in press) also emphasized the importance of crew comfort; successful tracking demands an alert crew since tuna can swim faster than the boat for short periods of time. If a fish is lost the crew must be aware of its escape direction to relocate it.

Since the boat is usually within about 1 km of the fish, horizontal position of the boat and the tracked fish is considered the same; positions are usually taken every 30 to 60 min. The pulse interval of the tag is converted to depth or water temperature by applying conversion factors determined by calibration. Generally these measurements are made at 1-3 minute intervals either by laborious counting by ear and timing with a stop watch, or automatically by pulse interval or frequency counters. Holland et al. (in press) employed a tape record to make a permanent record of the track for later analysis with a pulse interval meter connected to a microcomputer. From these measurements and temperature-depth profiles taken by expendable bathythermograph, temperature and depth distributions are constructed for each fish. Total path swum is considered to be a sum of movements between depth position to depth position along the hypotenuse of a triangle projected on a vertical plane whose horizontal leg was determined from 30-60 minute position information. Swimming speed estimates are thus an improvement over those obtained from just horizontal movement, but are still underestimates of true swimming speeds especially when the fish make frequent brief changes in heading. Estimates of swimming speed are, of course, most accurate during periods of relatively fast movement on a steady course.

3.5.2 **Tuna Tracks to Date**

Fifty-three successful tracks of tunas have been reported as of August 1985 (Table 5). The tracks averaged 26.75 hrs, ranging from 1 hr to 10 days, although the two longest tracks reported (168 hrs, Yuen 1970 and 144 hrs, Holland et al. [in press]) were intermittent tracks where the fish was either lost or abandoned and relocated later. Only reported tracks are considered here, although other unreported, and presumably unsuccessful (i.e. very short), tracks exist. Carey and Lawson (1973) mention five bluefin tracks that were of adequate duration (presumably), but they presented no data because the fish remained in water of constant temperature and they were interested primarily in thermoregulatory behavior.

The first successful tracks of tuna were by Yuen (1970); he tracked two skipjack in the waters off the island of Oahu, Hawaii. A notable feature of these tracks was the striking ability of the fish to move away from and return to a precise location each day. The skipjack spent the day on a shallow bank; within a couple of hours of sunset, they swam away from the bank on a fairly straight course until about 2 AM (local standard time), and then a more erratic swimming pattern was observed. Although the fish swam away from the bank by different courses each night, it was usually back at the same location on the bank by sunrise. Yuen (1970) believed that the fish swam faster at night.

Table 5

Successful ultrasonic tracking of tunas.

Species	Size	Month/Year	Area	Duration (hr)
Yuen (1970)				
Skipjack	44 cm	8/1969	Kaula Bank, HI	168
Skipjack	40 cm	8/1969	Penguin Bank, HI	12
Carey and Lawson (1973)				
Bluefin	230 kg	8/1969	St. Margaret Bay,	6
Bluefin	270 kg	7/1970	Nova Scotia	22
Bluefin	270 kg	7/1970	"	13
Bluefin	230 kg	7/1970	"	24
Bluefin	270 kg	7/1970	"	32
Bluefin	230 kg	7/1970	"	56
Bluefin	230 kg	5/1970	38°N, 71°W	23
Bigeye	70 kg	10/1970	39°N, 70°W	17
Laurs, Yuen and Johnson (1977)				
Albacore	84 cm	8/1972	36°N, 122°W	28
Albacore	87 cm	8/1972	36°N, 122°W	41
Albacore	85 cm	8/1972	36°N, 122°W	50
Dizon, Brill and Yuen (1978)				
Skipjack	70 cm	5/1977	Penguin Bank, HI	24
Skipjack	70 cm	5/1977	"	11
Skipjack	70 cm	5/1977	"	10
Carey and Olson (1982)				
Yellowfin	87 cm	4/1981	8°N, 79°W	9
Yellowfin	89 cm	4/1981	8°N, 79°W	46
Yellowfin	98 cm	5/1981	10°N, 109°W	18
Yellowfin	96 cm	5/1981	10°N, 109°W	48
Yonemori (1982)				
Yellowfin	63 cm	11/1981	1°S, 158°E	9
Yellowfin	68 cm	11/1981	1°S, 158°E	8
Yellowfin	70 cm	11/1981	1°S, 158°E	15
Yellowfin	64 cm	11/1981	1°S, 158°E	32
Bard and Pincock (1982)				
Skipjack	44 cm	7/1981	5°N, 0°E	3
Skipjack	45 cm	7/1981	2°N, 4°E	7
Levenez (1982)				
Skipjack	55 cm	11/1981	9°N, 21°W	44
Skipjack	53 cm	11/1981	9°N, 21°W	19

Table 5. (continued)

Dotson (personal communication)				
Albacore	73 cm	7/1979	31°N, 119°W	31
Albacore	86 cm	7/1979	31°N, 121°W	29
Albacore	76 cm	9/1979	32°N, 121°W	8
Albacore	88 cm	7/1980	32°N, 121°W	12
Albacore	86 cm	8/1980	32°N, 121°W	7
Albacore	82 cm	8/1980	32°N, 121°W	1
Albacore	87 cm	8/1980	33°N, 120°W	3
Albacore	80 cm	8/1981	33°N, 124°W	11
Albacore	79 cm	8/1981	33°N, 124°W	23
Albacore	68 cm	8/1981	33°N, 124°W	15
Albacore	83 cm	8/1981	33°N, 124°W	22
Albacore	80 cm	2/1982	31°N, 139°W	14
Albacore	85 cm	2/1982	31°N, 139°W	25
Holland (personal communication)				
Bigeye			Leeward Oahu, HI	24
Bigeye			"	28
Yellowfin			"	5
Yellowfin			"	24
Yellowfin			"	48
Yellowfin			"	9
Yellowfin			"	12
Yellowfin			"	14
Yellowfin			"	40
Yellowfin			"	144
Yellowfin			"	36
Yellowfin			"	38
			AVERAGE TRACKING DURATION	26.75

Carey and Lawson (1973) were interested primarily in demonstrating that bluefin were capable of physiological thermoregulation. They used temperature-sensitive sonic tags and published only the tracks in which bluefin showed an inverse thermal response to water temperature changes, i.e. water temperature decreasing, fish temperature constant or increasing. Some of the published tracks did show what was later found to be a common tuna behavior, namely, dramatic and frequent vertical excursions. The fish made abrupt dives periodically from surface water of 18°C to the thermocline at 4-5°C.

In 1972 Laurs et al. (1977) tracked albacore and, for the first time, complete oceanographic measurements were taken by a second vessel to correlate fish movement with habitat. They observed that albacore concentrated in the vicinity of upwelling fronts (for feeding?) and moved away from an area when upwelling ceased and the front disappeared. The albacore also seemed to avoid water where the surface temperature was below 15°C.

Dizon et al. (1978) employed depth-sensitive, rather than temperature-sensitive, tags for tunas. They tracked three large skipjack and described the characteristic vertical diving and ascending behavior and modal depth, temperature and swimming speed values. Dives were noted from the surface to as deep as 273 m; during the day, their modal depth was in the lower part of the mixed layer, but at night the fish spent more time near the surface, and extreme vertical excursions were much less common.

Carey and Olson (1982) observed that yellowfin in the eastern tropical Pacific swam in the region between the surface and the bottom of the thermocline, but spent most of their time in the upper part of the thermocline, and occasionally made very deep dives--one fish dove to 464 m (Figure 19). They noted that the tracked yellowfin spent little time at the surface, and suggested that feeding yellowfin might spend more time in the mixed layer but migrating or non-feeding fish would be found in the thermocline. This concept of a characteristic depth used when migrating would be observed by later investigators.

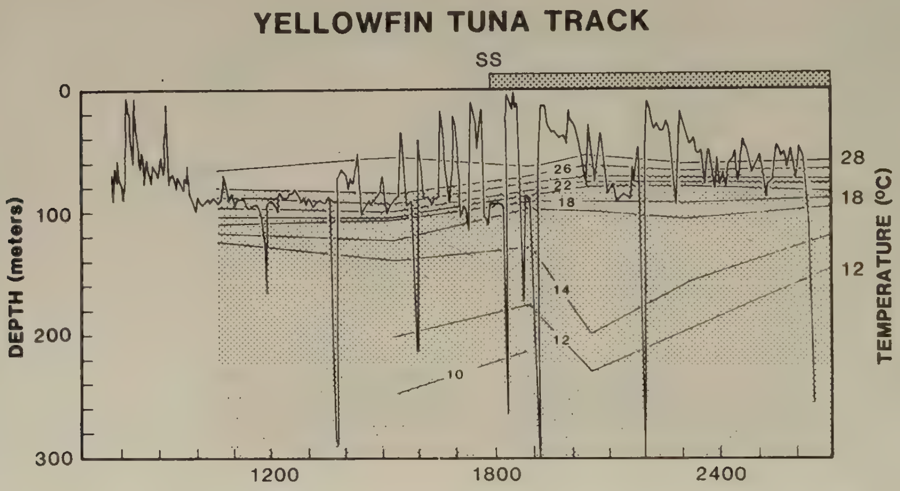
YELLOWFIN TUNA TRACK

Figure 19. Vertical projection of a track of a 98-cm yellowfin tuna (#4, 12-13 May 1981; redrawn from Carey and Olson 1982). This fish was tracked for 18 hours near Clipperton Island (10°N, 109°W). At 0225 hours this fish dove to 464 m. SS is sunset. The stippling denotes water below the top of the thermocline.

Yonemori (1982) successfully tracked four yellowfin somewhat smaller than those of Carey and Olson (1982) in the western Pacific around "payaos," a Philippine fish aggregation device. He observed similar, very active, vertical excursions. The deepest dive was to 200 m. At about an hour before sunrise, the fish made an abrupt transition from a modal depth (50 m) in the mixed layer (29°C) to a modal depth (175 m) in the middle of the thermocline (22°C) (Figure 20).

Bard and Pincock (1982), tracking two skipjack in the Gulf of Guinea, noted that the thermocline or some associated property limited vertical movements to the upper 50 m (17°C). In contrast, Levenez (1982) observed spectacular diving behavior in two somewhat larger skipjack tracked west of the Gulf of Guinea. One fish preferred a modal temperature of 28°C, but periodically dove to below 14°C. The other fish also spent the majority of its time in the upper mixed layer where the water was quite warm (24-28°C), but deep dives were persistently made--to more than 400 m where the temperature was 9.5°C and the oxygen was less than 1.5 ml/l.

The 6 albacore tracks from the North Pacific demonstrated that their behavior, like that of other tracked tunas, is characterized by dramatic and frequent vertical excursions (Laurs et al. 1980; Dotson pers. comm.). They noted that albacore, like skipjack, swam deeper during the day, but in

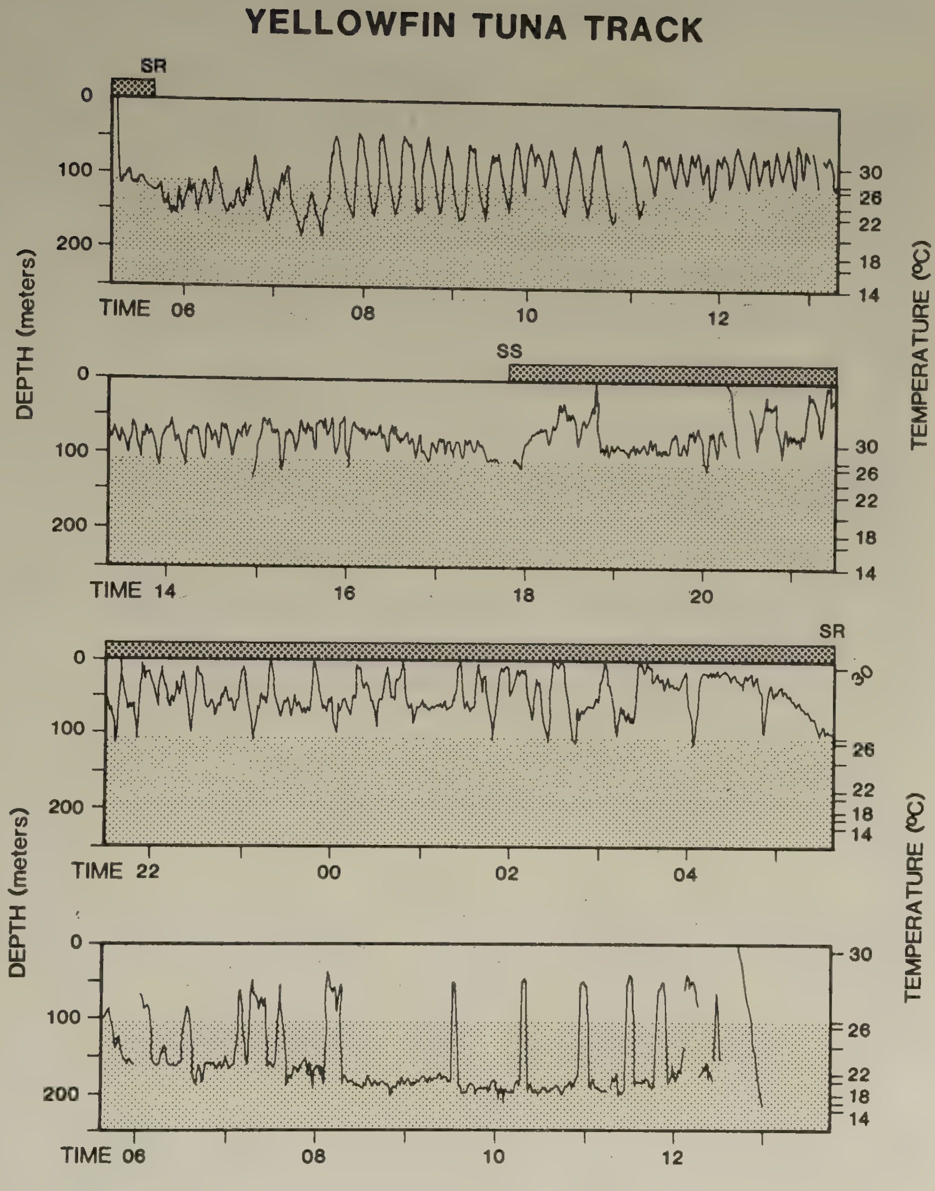

Figure 20. Vertical projection of a track of a 64-cm yellowfin tuna caught around a payao (redrawn from Yonemori 1982). This fish was tracked for 32 hours in the vicinity of 0°55'S, 157°53'E. Toward the end of the track, the fish spent the majority of the time well below the thermocline. SS is sunset and SR is sunrise. The stippling denotes waters below the top of the thermocline.

contrast to skipjack, spent most of the time in the upper thermocline. Albacore apparently oriented to a seamount in a manner similar to that described by Yuen (1970) for small skipjack orienting to banks.

Holland and co-workers (NMFS, Southwest Fisheries Center, P.O. Box 3830, Honolulu, HI, 96812) have tracked tunas over the past 2 years usually on the leeward (southwestern) side of Oahu, Hawaii, using a small (10-m) vessel. The combination of protected waters, a highly-efficient tracking vessel, refined tracking techniques (Holland et al. in press), and a system of fish aggregation devices (FADs) have yielded excellent results (Holland pers. comm.). To date, 10 yellowfin and 2 bigeye have been followed, and their behavior is essentially the same as that reported in previous studies: abrupt vertical migrations, modal depth in the upper thermocline or lower mixed layer for the yellowfin and the lower thermocline for the bigeye, and precise orientation to specific features (payaos, banks, or seamounts). The bigeye also demonstrated highly periodic, similar ascents from depth. Supported also is the concept of migrations occurring at depth and the fish shoaling at night.

3.5.3 Uncertainties

Some uncertainties exist in the interpretation of tracking records. A key issue is whether the behaviors noted are normal or the result of trauma caused by the attachment of the tag or disturbances produced by the tracking vessel. Holland (pers. comm.) was told that a fisherman had recovered, by trolling, a transmitter-tagged fish which had been at liberty 3 weeks. The fish obviously was healthy enough to feed and appeared normal (except for the tag) to the fisherman. Also, many of the investigators reported that their transmitter-tagged fish had joined a fish school.

Another caveat to any generalizations drawn from the data is that the tracked fish represent a relatively narrow size range of the representative species. There is no way of knowing if the behaviors observed, particularly the dramatic vertical excursions and the modal or preferred temperature, are typical of the large size classes of the various species, since data exist (except those of Carey and Lawson 1973) only for the smaller individuals.

Swimming speeds estimated from the horizontal and vertical components of a tuna movement vector are minimums. Small horizontal excursions not observable from the tracking vessel might be a significant portion of the total energy expenditure. In fact, the estimated swimming speeds from ultrasonic tracking work generally are below Magnuson's (1973) theoretical minimum for maintaining hydrostatic equilibrium during horizontal swimming.

3.5.4 Management Implications

Holland and co-workers (pers. comm.) and Yonemori (1982) attached transmitters to tunas to examine behaviors in association with FADs. Holland suggested that a knowledge of horizontal movements between and around various aggregation devices would enable managers to be more effective in FAD placement, and density, depth of placement, and fishing strategies could be evaluated.

Tracking data also seem useful for directing fishing effort, since information on habitat preferences could be used to determine fishing depths and temperatures. Tracking information could also be used to describe escape responses when tuna are encircled by a purse seine. Drawing on observations that purse seining is less effective in the western as opposed to the eastern Pacific, Green (1967) suggested that vulnerability to a purse seine is markedly reduced when the thermocline is deep because tuna avoid swimming into or through the thermocline, but tracking information contradicts Green's (1967) explanation. Yellowfin tracked in the eastern and western Pacific (Carey and Olson 1982; Yonemori 1982) show no reluctance to penetrate and inhabit the thermocline (Figures 19 and 20).

Ultrasonic tracking also provides critical data for the construction of energy budgets and growth models. Transmitter-equipped fish provide the only source of information on distribution of swimming speeds, and hence estimates of daily energy requirements. Perhaps most important, tracking provides accurate information on the vertical movements and distribution, a key information need for virtually all work on movement dynamics of tunas.

3.5.5 Conclusions

Four concepts concerning small-scale movements of tunas of the size range and species tracked have emerged from the tracking efforts to date:

(1) Tracking records of tuna demonstrate persistent, frequent, rapid and extensive vertical excursions. Owing to the rapid rate of descent or ascent, (records have a characteristic spiky appearance) the fish is submitted to rapid and large temperature and pressure changes. This must affect its ability to sense and respond to subtle horizontal temperature differences. Speculations on the use of these horizontal temperature gradients for orientation must be tempered by this observation.

(2) At night the modal depth of tuna shoals usually shifts from deeper layers to layers near the surface, and sometimes this is characterized by heightened vertical excursion activity at dawn and dusk.

(3) Several investigators (Carey and Olson 1982; supported by Holland pers. comm. and Dotson pers. comm., NMFS, Southwest Fisheries Center, La Jolla, California, USA) suggest that migrating tunas make fewer vertical excursions and maintain a lower modal depth than fish believed to be feeding. When tuna are maintaining a steady compass heading, fewer vertical excursions are noted. Identification of a species-specific traveling or migrating depth range or temperature range would be extremely useful, and present reports indicate that they may exist for certain habitats. Work by Laurs and Dotson and by Holland et al. may clarify this point when published.

(4) Cursory inspection of the illustrations of the tracking records indicates that the modal temperatures experienced by the various tagged fish appear to be very different. Striking differences in temperatures experienced by the fish appear to exist between day and night. Also abrupt shifts in modal depth or temperature were sometimes seen in fish in the same area and even in the same fish. It would have been instructive to summarize these modal depths and temperatures, but most of the authors do not provide such data.

Holland et al. (pers. comm.) speculated that the persistent vertical excursions have a thermoregulatory function, and serve to provide a more consistent internal temperature since internal temperature lags the water temperature, especially in large fish, (Neill and Stevens 1974; Stevens and Neill 1978). For example, many excursions into cool, deep water could compensate for high levels of feeding activity in the warm water of the mixed layer. Or frequent ascents into the mixed layer could, in contrast, compensate for relatively lower activities as the fish migrates in the thermocline. We suggest that the relationships developed by Neill and co-workers (Neill and Stevens 1974; Neill et al. 1976; Dizon et al. 1978; Stevens and Neill 1978; Dizon and Brill 1979, a) for estimating internal body temperature based on size, activity, and water temperature could be applied to time series of swimming speeds and water temperatures obtained from the tracks to examine changes in the theoretical internal temperature.

It might explain the seemingly chaotic ambient temperature changes apparent in the tracking record and show that the persistent vertical excursions are indeed behavioral thermoregulation.

4. POTENTIAL TECHNOLOGY

In the following three sections we discuss techniques which might be applied or are beginning to be applied to the study of tuna movement dynamics. These technologies include development of new tagging systems, measurement of physiological state, and reconstruction of movement histories from microconstituents of mineralized tissue.

4.1 Future Tagging Systems for Tuna

Of considerable importance to the study of the movements of tunas are tagging systems that might be used to: 1) increase the recovery rates over those of conventional tags; 2) assure that complete and correct data are secured for each tagged fish recovered; 3) provide a fishery-independent system that identifies fish position; and 4) extend our knowledge of the paths followed by tunas beyond the time and space limits of tracking individual fish using acoustic tags (about 3 to 5 days, 300-1000 km).

Six tagging systems or approaches are discussed here in varying degrees of detail. This is not an exhaustive list, but merely the systems which emerged from our discussion. The systems we describe differ in the degree of practicality, costs, and applicability to specific fisheries or fishery problems. We occasionally give approximate costs in U.S. dollars (1985) of tagging equipment or of research and development. These are merely the best guess of the panel and experts. The subject of telemetry systems is also reviewed by Mitson (MS).

4.1.1 Fishery-dependent, Auto-detectable Systems

An ideal fishery-dependent tag recovery system is one in which the identity code of a marked fish and possibly other data (position of vessel and time of capture) are automatically recorded when a fish is caught. No such tagging system presently exists, nor it is likely that one will be developed in the near future. On the other hand, automatic tag detection systems exist and an automatic reading tag is under development for salmon. Each is discussed below.

(1) Coded Ferromagnetic Implanted Tags

Tuna tags are recovered by fishermen, unloaders and cannery workers, who are requested to return them to fishery agencies along with data on date of capture, fish size and other details. Tags are often recovered but are not returned or returned with incomplete or incorrect data. This problem could be eliminated with the use of hidden tags which are detected automatically. Existing systems in salmon and herring fisheries, developed by Northwest Marine Technology (Shaw Island, Washington, USA; Jefferts et al. 1963) allow the injection of coded, magnetically-detectable tags into juvenile or possibly larval fish. These inert tags remain in the tissue and are recovered upon capture; recovery involves either an automatic system which, when triggered by a magnetometer scanning the conveyor belt in the processing plant, diverts a portion of the catch for examination, or a hand-held magnetometer used to examine the catch for tagged specimens.

Depending on the size of the tag (< 1 mm and up), binary codes are permanently etched or notched into the inert tag material. After the tagged fish is identified, the tag is dissected from the fish and read under a microscope. Alternatively the fish head can be x-rayed and the code (notches) read in the radiograph.

Costs of the tags (about $0.15 each for individually coded tags) and a hand-held tagging gun (0.5-1.0 K$) are modest, but the cost of an automatic tag detection system that could be installed in a tuna cannery would be expensive (75-100 K$), require research and development, and be practical only for some canneries. A hand-held magnetometer (3 K$), with which the port sampler scans the fish while they are being unloaded, would be more practical for tuna.

(2) Passive Integrated Transponder (PIT) Tag

The PIT system, developed by Identification Devices, Inc., Westminister, Colorado, USA, is currently being evaluated as an automatically-read tag for salmon (Prentice and Park 1984). The tag automatically transmits the identity codes of salmon as they move at 3 m/s through a 30-cm dia. tube; 94% readability has been recently obtained (E. Prentice, pers. comm., National Marine Fisheries Service, Manchester Fisheries Research Laboratory, Manchester, Washington, USA). The PIT tag is small (10 x 2.1 mm) and has no power source, but responds to a strong radio frequency (RF) pulse with a serial message. The RF pulse provides power to the circuitry for the message transmission. The fish identification, of course, is encrypted in the message. The tag is presently injected intraperitoneally with a hypodermic syringe; laboratory work indicates tag implantation produces no noticeable effects on growth or incidence of disease in salmon (Prentice and Park 1984).

The PIT system would be impractical for tunas at present because of its short detection range (7.5 cm) and high cost of development, but technological developments might make the system practical in the future. Development of the PIT system for salmon is proceeding under the supervision of Earl Prentice (address given above), and it is anticipated that a pilot installation for salmon will be functional by the summer of 1985.

4.1.2 Tags That Indicate Geographic Position

A major information gap exists between the short (1-3 day) highly-detailed paths of acoustically-tracked tunas and the two position points recorded for marked and eventually recaptured fish. Many (Joseph and Wild 1984) have recognized the need for combining the advantages of the two approaches. The major barriers to expanding the time scale and coverage of acoustic tracking of tuna are: crew endurance (3-5 consecutive days is the maximum that can be expected of a single crew) and vessel costs (at present the limit is one fish tracked per vessel). The life of the present commercially-available acoustic tags (20 or more days) is far beyond the endurance of a single crew. As endurance is increased by using bigger vessels and larger crews, cost mounts precipitously. We discuss below the advantages and disadvantages of three potential systems that could increase the number of fish tracked and the duration of the track. A more detailed technical discussion of the limitations of acoustic and satellite tracking systems is provided by Priede (1986).

(1) Sonobouy-Transponder Systems

A system composed of a number of small floating receivers in fixed positions and transmitters attached to many fish would be practical under certain conditions. When a transmitter-equipped fish swam within the range, the receiver would record or rebroadcast the identity code of the fish. Conventional pulsed ultrasonic tags would be impractical for this application because their range would be too short, since the system would probably be based on an omnidirectional hydrophone. A scanning hydrophone would greatly increase costs. Detection range could be increased to some extent by using transponding tags on the fish. Transponders have the advantage of longer life (the transmitter transmits only when queried) and larger range, since signal-to-noise ratios are improved because of the relatively precise relationship between the query signal and the return from the tag.

Inexpensive ($200) anti-submarine warfare (ASW) sonobouys could be used as receivers; ASW sonobouys are wide-band ultrasonic receivers which rebroadcast the received acoustic signals on very high frequencies (VHF) to stations located within line-of-sight of the buoys. However, extensive modifications would be required for their use in a transponder system: a transmitter would have to be installed to query the area periodically for the presence of tagged fish; the receiver section would have to be modified from wide-band to a narrow frequency band centered on the tag's frequency; and the buoy transmitter would have to be altered to retransmit on frequencies other than the ASW ones, or if the system needs recording capabilities, those would have to be installed. These modifications of the ASW sonobouys would probably cost $1000-$3000 per buoy.

The transponding fish transmitters were estimated to cost from $100 to $500 each and have a query range of about 0.5 to 1.0 km from the omnidirectional hydrophone. Receiver costs severely limit the number that could be deployed, and thus restrict the system's use to situations where the expected fish path is circumscribed or the presence of fish in a particular area needs to be ascertained. The system could be used profitably in situations where fish remain near fish aggregation devices.

(2) "Pop-up" Tags

A tagging system in which the tag surfaced after a specified condition was met (elapsed time, mortality, etc.) and "reported" its position could be a powerful tool. Such a fishery-independent tag recovery system would solve many problems related to tuna movement, including incomplete and erroneous data furnished by fishermen or others, and tag loss through emigration out of the fishery, or mortality. While such a system is easily conceived, realization is technically difficult. In addition, because the system described here would provide only two geographic positions, tag unit cost must be relatively low.

Electronically-controlled fusible links that could release the tag are available now (Nelson and McKibben 1981; J.M. McKibben pers. com., Ultrasonic Telemetry Systems, 8315 Millikin Ave., Whittier, CA, USA). The cost of such release systems (about $100), size (about 2 x 5 cm including battery) and precision of release and transport to the surface (0.5-1h) would allow a design of a practical system.

Position reporting could be done most cheaply by relying on aircraft. From the air, a VHF signal transmitted by the tag when it reached the surface could be detected along a track 300 nm wide. Knowledge of the precise time of release would limit aircraft costs. We believe that $200 per tag (including release mechanism) could be realized. Although no technical barriers exist to the development of such a tag, they are not in commercial production and we believe that research and development costs would be substantial.

Ideally, position could be reported via ARGOS satellite. The advantages of satellite recovery of information are obvious and, if a "mortality" pop-up could be incorporated, the data would be of great value in resolving issues related to natural mortality and emigration of tunas.

On the other hand, present size (100 mm dia., 250g) and costs of ARGOS transmitters ($2000 each) exclusive of the timed-release component (see above) make satellite reading of pop-up tags impractical at present. It also seems unlikely that cost will substantially decline in the near future because of the high cost of the precision oscillator used to transmit the signal to the satellite (less than 2 Hz drift out of a mega Hz causes rejection by ARGOS). Nor are great reductions in size likely because of the high (2 watt) power requirement for transmission (the battery makes up about two-thirds of the tag weight). Thus, because of their cost and size, satellite tags seem an impractical system for tracing tuna movements at present. On the other hand, satellite tags are an area of intensive experimentation (Mitson MS), and substantial reductions in size and costs have already been accomplished. In the unlikely event that substantial reductions occur in the future the pop-up satellite tag for tuna should be reconsidered.

(3) **Archival Position-Recording Tags**

Northwest Marine Technology, Inc., has completed a feasibility design for a miniature (1 cm x 6 cm) tag which allows storage of 8k bytes as a function of elapsed time. The tagged fish could remain at large for 5 years, the useful life of a lithium battery, but data collection can extend over only one year because sufficient battery power (about 1 microwatt) must be reserved to maintain data in the memory. The tag would collect data from three environmental sensors (ports) and record them and elapsed time for eventual reading when the tag is recovered by the fishery. The tag is, essentially, a highly-compact, low-power consuming microprocessor. Its greatest advantage lies in the ability of the user to configure its software and its sensors to meet a variety of experimental situations. Although the development cost of such a tagging system is substantial, Northwest Marine Technology has indicated it would develop the tag if a $100K commitment to purchase tags were made (satisfactory tag performance guaranteed before payment). The number of tags included in the initial contract would be 100 or more, depending on tag size, software and other specifications.

While collection of environmental data, such as temperature and depth, over extended periods would be extremely useful in answering specific behavioral and physiological questions, the most important application of the tag is that it could record a series of geographic positions and still collect temperature and depth information. Longitude can be accurately determined by including a photoresistor and measuring the Greenwich time of sunrise, and latitude can be determined from depth-specific seawater temperatures. As 8k bytes can be stored by the ultra-miniature tag, it could record 3 data items 7 times per day for a year or equivalently 50 times per day, one day per week for a year.

Recognizing that recoveries decrease geometrically with time, data acquisition rate could be easily programmed to be non-linear (programming of sampling intervals can be done after the tag is constructed). For example, initially data could be collected and stored at hour or half-hour intervals until the memory was filled, and then the acquisition rate could be reduced to intervals of a week or fortnight and the new data would be stored over the old (retaining sufficient amounts of the old data so that the time series remained complete). In this manner highly detailed daily records of depth, temperature, and position could be recorded during the period that returns from the fishery are the most likely (the first 100 days at large) without losing valuable position data inherent in long-term recoveries.

A simulation study of the precision of latitude estimates was completed by Smith and Goodman (1986). Each fish position was considered independently and the precision was a function of the variance in the long-term mean depth-temperature relationship for a particular time of year. The simulation indicated that the minimum precision that could be expected using temperature and depth data recorded by the tag was within 5 degrees of latitude. The precision of the longitude estimate is a function of the interval of time used to measure sunset and sunrise and therefore is under the control of the experimenter. Resolution on the order of one degree could be readily achieved. Five degrees of latitude is the minimum precision that could be expected, as the model is very conservative. Taking into account the previous position of the fish, and having real-time oceanographic measures of surface temperature from satellites and other sources could increase the precision 2 or 3 fold.

(4) Archival Pop-up Tags

The ideal tag would be a data recording tag as described in the previous section that surfaced and reported the data to a satellite at a specified time. This tag is essentially a marriage of the two systems previously discussed (pop-up and archival position-recording tags). The high unit cost of such a satellite tag might be acceptable in this case because many fish positions as well as a wealth of environmental data would be acquired rather than a single fish position determined from satellite. In addition such a system would be truly fishery independent, and the rate of recovery of information would be high.

The chief problem with such a tagging system is that the message length permitted by ARGOS is far too short to utilize the unique features of the archival tag because ARGOS would permit only a few data points to be transmitted. The short message length is a necessary feature of ARGOS, which is a low-altitude satellite that moves rapidly across the horizon. The low altitude reduces the power transmission requirements and the short message length enables many users to share the same satellite. The high-quality oscillator, an important cost factor in an ARGOS compatible tag, is not strictly necessary if location of the tag by the satellite is not required as would be the case for an archival tag. However, ARGOS will not permit such a degradation since the fine frequency separation is used to monitor several transmitters simultaneously.

An important step in development of such a tag would be to develop a new set of satellite specifications and determine if they could be accommodated within the NOAA satellite program. Data archiving requires a much larger data capacity than is normal and a satellite channel might have to be specially dedicated to monitoring such tags. Some oceanographers in the NOAA program are advocating longer message lengths for ARGOS, so development of such a tag may be possible in the future.

Thus a pop-up, data recording tag for tunas is technically feasible if an accommodation can be reached with satellite specifications. In fact, the Lowestoft Laboratory (Directorate of Fisheries Research, Ministry of Agriculture, Fisheries and Food ; United Kingdom) has taken up the challenge to significantly reduce the size of a satellite transmitter to meet the requirements for a pop-up satellite tag for tuna. A study is underway for the design of a data storage tag which can be incorporated into the pop-up satellite tag. This also includes an investigation of methods for position finding and recording. Final designs and specifications should be achieved in 1986 (R. Mitson, Lowestoft, U.K., pers. comm.).

4.1.3 Conclusions

The ideal tag recovery system in which the identity code and position and environmental history are automatically recorded is presently impractical. No system presently exists that will automatically read fish identity codes when fish are captured or processed, but the PIT tag is a first step. On the other hand, a tag that stores data on fish position and the environment which is recovered when the fish is recaptured (archival tag) is practical. Sonobouy-transponder systems and pop-up tags (detected by aircraft) might also be practical, but are of more limited use. The sonobouy-transponder system would probably be most useful in studying the behavior of tuna associated with fish attraction devices and the VHF pop-up tag might be used in areas where movements are greatly constrained by the coastline or when short-term recoveries are of interest. The costs of development might not justify the limited use of the VHF pop-up tag for tunas.

Of the systems considered in this report, we believe that the archival tag has the greatest potential. We believe that widespread use of the archival tag in conjunction with conventional mark and recapture studies would result in a quantum advance in knowledge of tuna movement dynamics. The ideal tagging system of this genre is an archival tag that surfaced and reported the data to a satellite (archival pop-up tag). The chief barrier to development of such a system appears to be a lack of compatibility with existing satellites, a problem that could be overcome in the future. For the present, we recommend development and testing of an archival tag in which the tags are recovered through the fishery. Tuna stocks for which tag recovery rate is high are the preferred stocks for the initial application of the tag. We also encourage a feasibility study of satellite recovery systems for an archival tuna tag.

4.2 Measurements of Physiological State

Interpretation of tag recovery data for estimation of movements, growth, and mortality would be aided by collecting information on the physiological condition of the fish at the time of tagging. Such measurements would help identify the factors motivating movement and regional and seasonal differences in life history characteristics. To date, fishery work has relied primarily on crude indices of condition, such as length-weight relationships and gonadosomatic indices, but the potential exists to infer much of a fish's present and past history from biochemical analyses and examination of tissue structure. Modern techniques, developed or being developed, allow or will allow determination of whether the physiological condition of a tuna is improving or deteriorating, its growth, swimming and feeding history, and its exact position in sexual maturity and many other characteristics (Love 1980). Such information would be invaluable for interpreting patterns and rates of movements of tunas and identifying the extent of heterogeneity in vital rate parameters (reproduction, growth, and mortality). Love (1980) lucidly summarizes this point of view and the existing literature on fishes. We briefly summarize below a few of the many possible approaches and provide some representative references.

4.2.1 Reproductive State

The gonadosomatic index is a useful measure of seasonality in reproduction in tunas (Orange 1961), although more informative techniques exist. A precise assessment of the female reproductive condition is possible by histological examination of formalin-preserved ovarian tissue from freshly-caught fish. When properly calibrated, identification and ageing of postovulatory follicles in active ovaries indicate time of last spawning (Hunter and Goldberg 1980). Alternatively, the incidence of females with hydrated oocytes can be used to estimate spawning frequency. In inactive ovaries, classification of atretic oocytes indicates time elapsed since the ovary was active (Hunter and Macewicz 1985). Frequency of spawning in tuna populations has recently been estimated for south Pacific skipjack (Hunter et al. MS) and black skipjack (Schaefer 1986).

Results indicated that south Pacific skipjack probably spawn nearly every day during peak spawning months and black skipjack every 2.5-4.0 days.

4.2.2 Growth

Measurement of recent growth (days to weeks) could be useful in interpreting differences in the pattern of movements among tagged fish or between areas. Several biochemical techniques are potentially useful as indices of recent growth; RNA/DNA ratios (Buckley 1984), polyribosome to monoribosome ratio (Lied et al. 1982); [14-C]-glycine uptake by scales (Smagula and Adelman 1983); and possibly messenger RNA (Somero and Lowery pers. comm., U. of California San Diego, La Jolla, CA, USA).

A number of publications describe the use of RNA/DNA as an index of recent growth in fish, and the technique has been successfully applied in the assessment of habitat quality for marine fish larvae (Buckley 1984).

Use of polyribosome to monoribosome ratios as an index of growth or nutritional condition (Lied et al. 1982) seems promising because the ratio would be much more sensitive to short-term changes than RNA/DNA. This technique is still in the developmental stage, however.

Uptake of [14-C]-glycine by the osteoblasts that remain attached to scales is another method that has been used to assess growth in fishes (Smagula and Adelman 1983), but the technique probably would require incubation on board ship and is less practical for tuna research than the other methods which require only that samples from live fish be frozen until returned to the laboratory for analysis. Calibration of any index with fish growth using captive fish is preferable, although an index of growth might be useful even without direct calibration.

4.2.3 Caloric Density

Analysis of fat concentration in tissues is one of a few biochemical techniques that have had widespread use in fisheries (Shul'man 1974), but rarely has it been applied to tunas or used for interpretation of movements. North Pacific albacore reduce their supply of fat during their transoceanic migration, and fat stores are replenished by active feeding prior to reaching the north American coast (Dotson 1978). Clearly, knowledge of caloric density would be quite helpful in interpreting movements of albacore.

Because the techniques are simple, the traditional approach to measuring caloric density in fishes has been to measure total lipid or water content. Boggs (1984) showed that the total lipid content in tunas is closely correlated with their water content. However, thin layer chromatography and flame ionization detection techniques make possible estimates of lipid classes (such as trigylcerides, cholesterol, free fatty lipids and polar lipids) in tissue samples as small as 25 g dry weight (Hakanson 1984). Fat profiles permit identification of changes in structural as well as storage lipids, and therefore are a more precise and informative measure of nutritional state. Also only small amounts of tissue need be collected, so the technique could be used to provide a precise measure of nutritional condition without damaging the fish at the time of tagging. It would be important to calibrate such work by determining a representative sampling location in the body as Boggs (1984) did for yellowfin.

4.2.4 Starvation and Energy Consumption

Many possibilities exist for assessing the degree of starvation and recent food assimilation rates. The time course of starvation-induced histopathology in larval fishes has been calibrated in the laboratory and used to measure the fraction of larvae dying of starvation per day in the sea (O'Connell 1980; O'Connell and Paloma 1981; Theilacker 1986). Some of these characteristics might be useful in adult tuna. For example, one might examine appearance of hepatocytes, glycogen concentration in the liver or the arrangement of cells in the pancreas (O'Connell 1980; O'Connell and Paloma 1981). Other potentially fruitful measures include activity of proteolytic enzymes in white muscle, fat content of the intestine (which might integrate ingestion events over 1-2 days), and the buffering capacity of muscle. In skipjack, histidine declines dramatically after less than a week of starvation (R. Brill pers. comm., NMFS, Southwest Fisheries Center, Honolulu, HI, USA). Since histidine is an important intracellular buffer in fish muscle, starved tuna with low histidine levels may be less able to cope with the proton load (from lactic acid) generated during burst swimming, and thus be more at risk.

4.2.5 Duration and Intensity of Activity

It seems likely that biochemical characterization of the musculature of tunas could be used to estimate the duration and intensity of previous activity. There is evidence in the literature of pervasive (weeks to months) biochemical changes in the locomotory musculature of mammals in response to exercise (reviewed in Holloszy and Booth 1976), and some evidence exists that similar changes occur in fish (Johnston and Moon 1980, 1980a).In addition, a correlation has been noted between glycolytic enzyme activities (lactate and malate dehydrogenase) of epaxial white muscle and routine metabolic rate in a variety of fishes (Childress and Somero 1979). Work in progress indicates that biochemical profiles (lactate dehydrogenase, citrate synthase, cytochrome-c oxidase activities, myoglobin concentration, and nucleic acid ratio) will provide indices of activity levels and growth and permit the calculation of feeding ration (S. Kaupp pers. comm., U. of California San Diego, La Jolla, CA, USA). Clearly, indices of past activity levels would be helpful in interpreting movements, estimating energy requirements and assessing fitness.

4.2.6 Mortality Risk

Natural mortality is a critical component in population models. Its estimation is useful in interpreting data on movements of tunas. For example, the expectation that fish released in area A will be recaptured in area B is dependent on natural mortality, as well as the movement from area A to B and fishing effort along the path between the areas and in area B. Natural mortality has been or might be estimated from results of large-scale tagging experiments (Bayliff 1971; Cayré, Diouf, Fonteneau, and Santa Rita Viera 1986), observed declines in year-class abundance, and various indirect mathematical manipulations (Beverton and Holt 1959; Hennemuth 1961; Pauly 1980). Such methods only approximate the actual natural mortality, and implicitly or explicitly assume that natural mortality is constant for all age classes recruited into the fishery despite the fact that it must be, by definition, age-specific. Clearly, measurements of the physiological state that collectively provide a profile of size-specific mortality risk would be a valuable addition to large-scale tagging experiments. It would be important in such an assessment of mortality risk to consider not only mean levels of such indices in sea-caught tuna, but the form of the distribution. For example, the distribution of RNA/DNA appears to be truncated in wild larval fish, with slow-growing individuals less abundant in the sea than one would predict from laboratory work (Buckley 1984).

Many of the indices described in the above sections would be appropriate elements in a mortality risk assessment. Also, some biochemical index of the ageing process would be a useful addition to other measurements. Such an index might be currently available by measuring the concentration of lipofuscin. Lipofuscin accumulates in tissues of a number of organisms in proportion to metabolic rate and, in some insects, a linear relationship exists between chronological age and lipofuscin concentration (Ettershank et al. 1983). Although not used to assess physiological or chronological age in fishes, it has been used to identify different cohorts of krill (Ettershank 1983). In addition to assessment of mortality risk, lipofuscin concentration might also find application in tuna movement studies as an index of chronological age of tagged individuals (via a small biopsy) or for identifying differences in metabolic processes between groups of tunas.

4.2.7 Summary

A few of many possible measurements of physiological state are summarized above. All appear valuable for interpreting tuna movements. Some, such as caloric density, RNA/DNA ratios and histological analysis of female reproductive condition, involve applying techniques used on other fishes to questions of interest to tuna biologists. The accuracy of most measurements would be improved by calibration experiments on live captive tuna. We believe that application of the existing techniques and development of new ones should be encouraged as part of a broad program on the dynamics of tuna movements.

4.3 Reconstruction of Movement Histories From Microconstituents of Mineralized Tissue

The tissues of fishes living in different environments are believed to acquire a unique chemical composition because of differences in local water chemistry, temperature, niche differences, and other characteristics of the environment. These differences in chemical composition are believed to be conserved in the skeletons of teleosts and constitute an ecological record because their bones are usually acellular (no osteocytes in the bone matrix), and the resorption of acellular bone is unlikely. New analytical techniques may make possible reconstruction of such histories. Work such as this could help identify the origins and size specific movements of tunas. Such work was not considered in our discussions because the formation of a separate working group has been proposed to evaluate the use of chemical constituents for age determination and estimation of stock heterogeneity and transfer rates of tunas (Joseph and Wild 1984). Although a thorough review was impractical, the panel believed that the potential of these methodologies was so great that some mention should be made of them here. For this short synopsis, we drew upon unpublished documents of T.J. Mulligan (University of Maryland, Chesapeake Biological Laboratory, Solomons, Maryland) and R. Radtke (Hawaii Institute of Marine Biology, University of Hawaii, USA) as well as the published literature

4.3.1 General Summary

To define movement patterns, otoliths or vertebrae may be preferable for microconstituent analysis because they may contain a record of the age of a fish as indicated by daily or annual growth increments, and perhaps more importantly, the constituents, once deposited, are likely to be stable and not resorbed as they are in scales (Mugiya and Watabe 1977). It is also preferable that the method be nondestructive and sensitive enough to determine the chemical composition within regions of estimated age on otoliths or vertebrae. Considering these criteria, the best method at this time appears to be X-ray fluorescence spectroscopy (Calaprice et al. 1975;

Mulligan et al. 1983). In this method the presence of elements is detected by measuring the energies of the X-rays produced when a section of an otolith or vertebrae is exposed to a high energy electron or proton beam. Because X-ray fluorescence is nondestructive, a sample can be run repeatedly and specific regions within the same skeletal part can be targeted for analysis. At the conclusion of the analysis, the data consist of an array of numbers, with each number corresponding to the total number of characteristic X-rays in a given energy range. From these X-ray energy spectra, the elemental composition is determined. The information can then be analyzed in various fashions, and the entire elemental profile or the relative concentrations of specific elements or their ratios can be used. Nonparametric or parametric pattern recognition techniques are applied to these data to identify groups or clusters of fish having similar chemical composition. The equipment, precision, analytical procedures, and statistical methods for microconstituent analysis in fishes have evolved considerably over the years, but some controversy still exists regarding the optimal approach to be used.

A number of recent studies have documented that chemical differences exist in mineralized tissues of fishes, and various pattern recognition techniques have been used to separate stocks of sockeye salmon (Calaprice 1971; Calaprice et al. 1971, 1975; Mulligan et al. 1983) and Atlantic bluefin (Calaprice 1986).

In addition to examination of such data for group similarities in elemental composition, it is theoretically possible to obtain a historic record of temperature changes experienced by the fish. The strontium-calcium ratio (Sr/Ca) in coral skeletons is negatively correlated with water temperature at the time of calcium deposition (Smith et al. 1979; Schneider and Smith 1982), and Sr may be substituted interstitially in the aragonite of fish otoliths in a temperature-dependent manner. Radtke and Targett (1984) found cyclic patterns in Sr/Ca in transects of the otoliths of an Antarctic fish; the cyclical patterns may be related to seasonal water temperatures. This apparent seasonality in the microconstituents of scallops and bluefin vertebrae was also noted by Calaprice et al (1971) and Calaprice (1986); his work is described in greater detail in subsequent sections. Recently, the Sr/Ca content in otoliths was determined for cod larvae reared in the laboratory at different temperatures. This laboratory calibration established that the Sr/Ca was a function of temperature, but that Sr was not deposited in equilibrium with inorganically precipitated aragonite (Radtke 1984). The slope of the relationship between temperature and Sr/Ca was the same as predicted with the equilibrium equation for inorganic aragonite, but the elevation of the line was much lower, indicating that metabolic processes probably controlled the amount of strontium incorporated into the otolith. Laboratory calibration on a species-by-species basis will probably be required to use Sr/Ca to reconstruct reliable thermal histories. It may be preferable to use a mix of more elements for more accurate temperature indicators, as shifts in the ratio of other elements with temperature, such as Cl/Br, can also be expected.

Stable isotopic concentrations of oxygen in fish vertebrae or otoliths may also provide a potentially useful historical record of the hydrographic environment experienced by the fish. For example, the isotope ratio of O^{18}/O^{16} seems to be an indicator of water temperature; oxygen is hypothesized to be deposited in otoliths in isotopic equilibrium with the surrounding seawater (Devereux 1967; Degens et al. 1969). Kolodny et al. (1983) found good agreement between temperatures deduced from O^{18} values in fish bones and water temperature and showed that isotopic concentrations were not affected by the concentrations in the food fed to the fish. If this is true for tunas, construction of a thermal history from isotopic analysis of the otolith may be possible.

The standard method of measuring the oxygen isotope ratio requires dissolving the sample and employing a mass-spectrometer, a destructive method complicated by the heterogeneous nature of the skeletal parts. Calaprice (1986) briefly describes an accelerator-based method he used to determine oxygen isotope ratios in bluefin vertebrae, which seems to eliminate these problems. In this preliminary study, vertebrae of juvenile bluefin from the western Atlantic had higher O^{18}/O^{16} ratios than did those from the eastern Atlantic, indicating that temperatures in their first winter were lower for fish in the eastern Atlantic. This result is reasonable since the temperature of the eastern bluefin nursery grounds in the Mediterranean can be 13°C or more cooler in winter than the western bluefin nursery grounds in the Gulf of Mexico. Similarly, Mulcahy et al. (1979) found that the O^{18} increased with age in a benthopelagic macrourid, indicating an ontogenetic movement into deeper, colder habitats, which agrees with field observations. However, the maximum depth predicted on the basis of the predicted temperatures exceeded the maximum depth (minimum temperature) of the species in the region studied. Thus, the equilibrium equation for O^{18} correctly identified the historical patterns of movement, but the estimated temperatures seemed inaccurate (R. Wilson, Scripps Institution of Oceanography, University of California at San Diego, pers. comm.). Temperature calibration of O^{18}/O^{16} ratios in larval cod otoliths in the laboratory has indicated that heavy isotope was not deposited in equilibrium with the surrounding environment, but that the deposition of the heavy isotope was temperature dependent (Radtke 1984). And similarly, oxygen isotope studies of otoliths of bluefin tuna held in captivity indicate that otolith carbonate was not derived directly from seawater bicarbonate (R. Radtke, pers. comm.). Clearly some biological processing of isotopes exists in cod, bluefin, and presumably other fishes; and species-specific O^{18} deposition rates must be calibrated before they can be used to reconstruct thermal histories.

4.3.2 Bluefin Stock Identification Using Microconstituents of Vertebrae

Recently, Calaprice (1986) analyzed juvenile (school fish) and adult (giant) bluefin tuna from fisheries in the western Atlantic, eastern Atlantic, and Mediterranean to estimate the degree of interchange of fish between eastern and western Atlantic fisheries. He used proton-induced rather than the more common electron-induced X-ray spectra to characterize the composition of inorganic elements of vertebrae. By analyzing 0.9-mm diameter sections of vertebrae, he produced linear transects of vertebral chemical composition from the center (area formed as juveniles) to the outer edge (area formed just prior to capture).

Ratios of elements such as calcium, strontium, phosphorus, sulphur, chlorine, bromine, and zinc varied cyclically as the vertebra was traversed from the center to the outer edge, indicating possible seasonality in deposition.

Comparisons of the chemical composition of vertebrae of bluefin from eastern and western Atlantic indicated that they probably intermix. The inferred degree of interchange was relatively low, with more fish immigrating from the eastern Atlantic to the west than the reverse. Of the 94 juveniles from the western Atlantic, 5.5% had patterns similar to the 131 fish from the eastern Atlantic, whereas none of the eastern Atlantic juveniles had patterns similar to those of the Western Atlantic. Similarly, the immigration of giant bluefin from the eastern Atlantic to the western Atlantic (inferred from chemical pattern similarity) ranged from 9.9 to 12.7% in two different years, and immigration from west to east was 2.6-9.9%.

4.3.3 Conclusions

The results for bluefin indicate that identification of chemical patterns in vertebrae has great potential for studying movement pattern. At present microconstituent analysis has been used primarily to identify the origins of the fish, rather than to provide a chronology of movements. Clearly, if chronologies of spatial movements can be resolved from chemical analysis, it would constitute a major breakthrough in tuna movement dynamics. Ideally, the chemical composition of specific habitats needs to be linked to specific chemical patterns in bones. This is not a straightforward problem as metabolic processes and biomagnification through food webs may substantially alter elemental composition of bones relative to their concentrations in seawater. Laboratory experimentation to identify such processes are needed, as are process-oriented field studies including microconstituent analysis of tagged fish recovered from the fishery. Further, chronologies are dependent upon the same assumptions and require the same validation as routine age estimations.

At this point the precision and power of the analytical techniques (chemical and statistical) have far outstripped physiological and environmental understanding of the processes. Laboratory studies are needed that confirm the conservation of induced chemical patterns in the vertebrae. Optimism is in order. Experimentally-induced hypercalcemia does not cause resorption of the bone of otoliths or vertebrae of fishes such as tunas which have acellular bone (Mugiya and Watabe 1977). Wendelaar Bonga et al. (1983) found that calcium and phosphate of opercular bones and fin rays were resorbed after treatment with a metabolite of vitamin D in a fish with acellular bone. Clearly, physiological processes do exist that could alter the microconstituent content of acellular bone. Although the physiological literature supports the hypothesis that microconstituents of acellular bone, under normal circumstances, are conserved, additional laboratory studies are needed to substantiate this assumption and to identify the extent metabolic processes are involved. Laboratory calibrations are also needed to verify that Sr/Ca, or O^{18}/O^{16} and other ratios of elements, are indices of temperatures experienced by the fish and to determine the correct temperature coefficients for tunas. Further, experiments are needed to determine the extent biomagnification affects elemental composition, for example by feeding fish food of known isotopic composition (Kolodny et al. 1983). These and other laboratory studies would strengthen the interpretations derived from chemical pattern analysis. Such laboratory work in conjunction with field studies could be done at relatively low cost, and even work on fishes other than tunas using key elements would help in this regard. It would also be important to include process-oriented work on chemical pattern chronology in any international program on tuna movement dynamics, as such a program could provide field validation for the method.

5. REQUISITES FOR RAPID ADVANCES IN KNOWLEDGE

For seven major tuna stocks we have documented the importance of increasing our understanding of the movements of tuna and we have identified the required information needs. Our review of existing fields of knowledge (mark and recapture, tuna oceanography, and ultrasonic telemetry) and potential, new technologies (tagging systems, physiological state assessment and microconstituent analysis) indicates that, although substantial progress has been made, major gaps remain in knowledge and technoclogy. A major theme of all of our deliberations was the optimal approach to increase the rate of knowledge acquisition. Knowledge and technology will continue to grow in the years to come, but the new demands on management of tuna resources make an acceleration of the present rate highly desirable. For rapid progress we believe increased effort in the following four areas is indispensable.

- Establish international arrangements to share tuna movement data, analyze movements on an oceanwide and worldwide basis and link the analyses to major international oceanographic programs.
- Increase the numbers and kinds of observations of the movements of tuna in the vertical plane.
- Develop and use technology for tracing the actual paths followed by tunas over extended periods and for measuring movements independent of the fishery.
- Conduct intensive studies on tuna movement dynamics which incorporate a wide range of disciplines and combine old with the new technologies that we have discussed.

Many research suggestions and information needs are mentioned throughout the text but we restrict our comments here to these four requisites. Each is discussed below.

5.1 Communications and Analysis of Historical Data

Creation of data files and wider distribution of existing files on tuna movement would foster broader understanding of tuna movements through inter-ocean analysis of movements; facilitate comparative studies of stocks; lead to more cooperation with less duplication of effort; and avoid the pitfalls of interpretation of movements from regional data. Three types of files--tag release and recapture, oceanography, and catch and effort--should be distributed to members of the tuna research community. Such communication is particularly important in the Indo-Pacific region. The establishment of a system for coordinated analysis of tuna movement data on an ocean-wide basis would be an important first step in developing an international research program on tuna movement dynamics.

The more obvious benefits of oceanwide sharing of movement data were discussed in detail in the section entitled "Reexamination of Tuna Movement Data" and require no additional comments. We consider here two of the less obvious benefits: use of the comparative method for understanding movements, and linking such data to new initiatives in oceanography.

5.1.1 Comparative Studies

An important opportunity exists for developing a better conceptual understanding of the movements of tunas by comparative studies of their movements using data from previous and current studies. For example, at present we cannot discern the extent differences in movement patterns among species and stocks is attributable to the environment or to species- and size-specific differences in movement patterns. Comparisons of estimates of various life history parameters among species and among stocks within species (including K of the von Bertalanffy growth equation and coefficient of natural mortality [Beverton and Holt 1959; Pauly 1980] and various physiological parameters [Sharp and Dizon 1978]) has been useful in developing conceptual understanding of stocks and species. Comparisons of parameters of movement estimated for as many stocks as possible have similar conceptual value. The simplest parameters are numbers of releases and returns and return rates--the latter divided by the former (Table 1). Tabulations of numbers of recaptures during various intervals, for example 0-30 days, 31-60 days, 61-180 days, 181-365 days, etc. at liberty and distributions of net distances travelled by fish at liberty for those periods (Kearney 1983) would also be useful. Other parameters which might be estimated and compared include A^2 and V (Table 2).

On a finer scale, standardizing the analysis of existing (and future) ultrasonic tracking data offers an important opportunity to advance fundamental understanding of tuna movement behavior by comparative study of behaviors with regard to depth and temperature among species, sizes, and areas. Most acoustic tracks of depth, temperature, or both are available only as pictorial graphs of swimming depth or temperature against time. Although these are valuable illustrations, they are not amenable to spectral analyses of the distributions of these parameters or to comparisons, except in a highly qualitative manner, between tracks, studies or species. We recommend that published reports provide distributions of temperatures or depths experienced by the fish and tabulated modal depths and temperatures. Some of this information could be recovered by digitizing the published graphs, and this would be a valuable exercise if reasonably accurate modal depths and temperatures could be extracted.

We recommend an effort to recover modal depth and temperature information whenever possible from previous data sets and strongly recommend that future investigators provide spectral analyses of the temperature and depth distributions of tracked fish stratified by day and night.

5.1.2 Integration with Oceanography Programs

Further analysis of historic catch and effort and tagging data using a broader concept of the features that affect vertical or horizontal distributions of tunas by affecting the aggregation or production of their forage seems warranted. For example, accurate models of the wind stress fields exist for some of the oceans and they could be easily developed for areas such as the southwest Pacific, where the models do not exist. Wind stress fields could be used to identify seasonal shifts in areas of convergence and divergence, as indicated by the zero wind stress curl. This analysis locates local areas of upwelling and increased productivity. The seasonal shift in forage or tuna movement might be examined profitably by plotting tuna distribution on moving coordinate systems based on an environmental parameter or an index of one, such as the zero curl line, an ocean front, or some other moving boundary. Such analyses would profit by consideration of vertical as well as horizontal dimensions. Regardless of the research approach, however, we believe establishment of linkages to existing and future broad-scale oceanographic programs, such as TOGA and WOCE, would be of great benefit.

5.2 Vertical Structure

For a major advance in the understanding or predicting of tuna movements, more data on the vertical structure of the habitat and the distribution of tunas within it are essential. The need for expanding our knowledge of vertical movements of tuna was a recurrent theme throughout our discussions. The present meager level of information needs to be expanded to include a greater size range of tuna and more habitat types. Sea-surface temperature and tuna distribution at the surface are only a crude index of events in subsurface layers, and better correlations would probably be obtained if vertical temperature structure and tuna distribution were better documented. At present we cannot measure vertical structure of the ocean from space, but recent advances in physical oceanography indicate that it may be possible in the future using satellite information and a historical understanding of the relationship between sea-surface temperature and deeper structure. Substantial progress will depend on tuna studies that examine the vertical distribution of tunas within the context of the vertical structure of the water column. Acoustic tracking of individual fish is the preferred approach. Although, using present technology, few fish can be studied, new technologies may increase the numbers and duration of tracks (see next section). Net displacement of groups is the most critical issue. Research gill nets and longline studies conducted with a knowledge of the structure of the water column also seem to be a promising approach that could be implemented using existing technology.

5.3 The Paths of Tunas Over Extended Periods

A key area for new technology is the development of devices that identify the paths of tunas in three dimensions over extended periods of weeks or months and provide a movement history independent of the fishery. Advances in very large-scale integrated circuit technology provide the potential of collecting detailed records of temperature, depth and geographical position in a tag to an accuracy of about 5 degrees of latitude and less than 1 degree of longitude in temperate waters (Smith and Goodman, 1986). Presently the most practical device of this type, the archival tag (see previous discussion), must be recovered to obtain the stored data, and thus is not totally fishery independent, although the position data is independent. Despite this limitation, we believe that the archival tag is an extremely important first step in development of tags to trace the movements of tunas independent of the fishery. We strongly recommend the development of this tag and initial testing in those stocks for which there are high rates of fishing mortalities and for which cooperation from fishermen, unloaders, and cannery workers can be expected.

5.4 Intensive Studies on Tuna Movement Dynamics

We believe that intensive studies on tuna movement dynamics which include, in addition to conventional mark and recovery of tunas, a wide range of disciplines and combine old with new technologies could lead to a fundamental advance in knowledge. Ideally, the experimental design of a major field study on mechanisms of tuna movement should contain mark and recapture, measurements of tuna in three dimensions, assessment of physiological state, microconstituent analysis of mineralized tissue, and measurement of the physical and possibly the biological characteristics of the habitat. Combining information from these five elements would provide the most powerful approach to defining movement and mixing of tunas among regions that modern technology can provide. Such a program would provide not only several independent measurements of movement in different time and space scales but a broad behavioral, physiological and environmental framework which could be used to interpret movement patterns and identify mechanisms.

A program of this kind would require development and testing of new methodologies (e.g. safe biopsies, storage of biological specimens and testing of new physiological state measurements) and new equipment (e.g. archival tags). Such work must be begun well in advance of the major investigation of tuna movement. For example, the definitive paper describing a test of the coded-wire tag for salmon was published in 1963 (Jefferts et al. 1963), but practical application to research and management problems took ten years. The techniques for tagging and recovery had to develop to a stage where managers were confident that large expenditures could be justified.

Each of the five major elements of this idealized program on tuna movement dynamics is briefly discussed below.

5.4.1 Mark and Recapture

Because of the large number of tuna movement trajectories that can be determined from the recoveries of the tags of a single cruise and the existence of extensive files of data, mark and recapture experiments must be central to any major study of tuna movements. The function of the measurements discussed in the following section is to enhance the ability to interpret the spatial and temporal patterns of recoveries of marked fish and possibly to reinterpret past data.

5.4.2 Movements In Three Dimensions

To correlate movements with habitat characteristics and to develop a fundamental understanding of the dynamics of tuna movements require an understanding of the pattern of movement in the vertical as well as the horizontal plane. Deployment of archival tags and conventional ultrasonic transmitters which collect depth distributions is needed. The latter are needed because, in many of the fisheries, insufficient numbers of recoveries of fish would make the archival tagging approach financially prohibitive. Archival tags, where practical, are far superior because long-term patterns of vertical movements would be provided, whereas acoustic tracking has been limited to less than a week and usually less than two days. Even a few recoveries of archival tags would provide extremely valuable information on the relation between migratory paths and habitat characteristics.

5.4.3 Physiological State

If more can be known about the physiological condition of tunas at the tagging and capture sites, then variation in movement patterns of individual fish, of groups of different sizes of fish, and variation in different regions, and during different seasons will be more accurately interpreted, as will the determination of vulnerability to various types of fishing gear. Even greater power of interpretation might be realized if the physiological state could be assessed from a non-damaging biopsy of the tagged and released individuals, rather than from sampling the school. A survey of the physiological state is essential because it is the only method for identifying likely motivating factors which form the basis of the observed movement patterns; this survey also might identify regional or seasonal heterogeneity in critical life history parameters, such as growth rate and mortality risk.

5.4.4 Microconstituent Analysis

A chronology of the microconstituents of vertebrae or otoliths of tuna captured in the course of the program would provide a method of assessing movement patterns and degree of mixing of tuna from different regions that would be independent of other methods (conventional tagging, tracking and/or records from archival tags). Thus, inclusion of microconstituent analysis in the program is strongly recommended. It would be particularly important to determine the chronology of microconstituents of the vertebrae of tagged tuna that were recovered in the course of the work; analysis of tuna that carried an archival tag for extended periods would be particularly valuable. Analyses of tagged fish might identify the very important links between habitat and chemical composition. An intensive program of this nature could provide the field validation needed for routine use of microconstituents in fishery work.

5.4.5 Habitat Characteristics

Measurement of the physical, and possibly the biological, characteristics of the habitat is essential for correlating habitat with observed movement patterns. In addition, real-time measurements of temperature structure of the water column, as well as surface temperature measurements by satellite centered on the tagging site and covering a broad area, would greatly increases the precision of the position estimates eventually obtained from the archival tag. Agencies involved in satellite image and data analysis need to be involved early in the planning stages to insure that adequate satellite coverage exists.

5.5 Need for Coordination

The idealized intensive program on movement dynamics we have discussed would have to draw from a broad scientific and institutional base. No single organization could marshal the resources to conduct such a program. Cooperative links would need to be established between government and institutional fishing agencies, the oceanographic community and academic researchers. Clearly the success of such a program would depend upon effective coordination among countries and organizations. Similarly coordination is essential for the sharing and distribution of existing data on tuna movements. Such cooperative activities would foster broader understanding of tuna movements through inter-ocean analysis of movements, facilitate comparative studies of stocks and help establish cooperative comparative studies on the same species of tuna in different oceans.

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7. ANNEX

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THE SPAWNING FREQUENCY OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, FROM THE SOUTH PACIFIC

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ABSTRACT

Histological criteria to age postovulatory follicles were developed from examination of laboratory-spawned skipjack tuna; the criteria were used to estimate the frequency of spawning of skipjack tuna from the South Pacific. Examination of 87 skipjack tuna from field collections taken in October-November indicated that spawning occurred nearly every day. The fraction of mature females with postovulatory follicles, <24 hours old, was 0.85 (standard deviation = 0.071) indicating that the mean interval between spawnings was only 1.18 days.

Estimates of the frequency of spawning of multiple spawning fishes are essential for understanding their reproductive biology. To estimate annual reproductive effort or fecundity, and how these variables are related to size or age structure of a population requires knowledge of the frequency of spawning and the number of eggs produced per spawning. Batch fecundity, the number of eggs produced per spawning, has been estimated for skipjack tuna a number of times (see review by Matsumoto et al. 1984) but the spawning rate of the skipjack is unknown. Thus spawning frequency is one of the missing links in an assessment of the reproduction of skipjack populations.

It has long been recognized that skipjack tuna spawn more than once in a season because more than one mode of advanced oocytes are found in active ovaries (Brock 1954; Buñag 1956; Joseph 1963; Raju 1964; Simmons 1969; Batts 1972; Cayré 1981; Goldberg and Au 1986). The frequency of occurrence of female black skipjack tuna, *Euthynnus lineatus*, throughout the spawning season with ovaries containing hydrated oocytes led Schaefer (1986) to conclude that the average interval between spawnings of black skipjack in the eastern tropical Pacific was 2.1-5.7 d depending on the region.

Over the last 6 years, two methods have been developed for measuring the spawning rate of multiple spawning marine fishes: One method is based on the frequency of ovaries containing hydrated oocytes and the other is based on the frequency with which they contain postovulatory follicles of known age (Hunter and Macewicz 1985a). These methods have been used to measure the rate of spawning in a number of marine fishes: *Engraulis mordax* (Hunter and Goldberg 1980; Hunter and Macewicz 1980); *Engraulis ringens* (Alheit et al. 1984); *Hypsoblennius jenkinsi* (Present 1985); *Sardinella brasiliensis* (Isaac-Nahum et al. 1985); *Seriphus politus* (DeMartini and Fountain 1981); and *Euthynnus lineatus* (Schaefer 1986). Postovulatory follicles were used in most studies, but DeMartini and Fountain (1981) and Schaefer (1986) used the incidence of females with hydrated oocytes to estimate spawning frequency. The hydrated oocyte method may produce a biased estimate in some species because of increased vulnerability of hydrated females to netting gear (Alheit et al. 1984).

The objective of this paper was to estimate the spawning rate of South Pacific skipjack tuna by applying some of these techniques. It was not possible to use the hydrated ovary method in our study because fish were not caught during the period of the day when the ovary was hydrated. Instead, we used the incidence of females having ovaries containing postovulatory follicles to estimate the frequency of spawning of skipjack tuna. This method requires ovaries to be preserved immediately in formaldehyde solution when the fish is caught, a histological examination of the ovary, and the development of a staging system for estimating the age of the postovulatory follicle. Our histological classification included not only an assessment of spawning frequency but also an assessment of the extent of ovarian atresia. The atretic condition of the ovary is a sensitive index of the reproductive state of

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females during the spawning season and can be used to identify females approaching the end of their spawning season as well as those in postspawning condition (Hunter and Macewicz 1985b).

METHODS

Skipjack tuna were captured either by pole and line or were catches associated with moored fish attraction devices or free floating natural flotsam. Two sets of collections of skipjack tuna were analyzed: a group of 12 females taken near Noumea, New Caledonia on 23 February 1984; and a group of 87 females taken in 8 different collections at various locations in the South Pacific from 20 October to 30 November 1984 (Table 1). Our samples were opportunistically taken and spanned a great latitudinal range (0°-23°S). At present the peak spawning months of skipjack tuna are poorly defined over this range of latitudes. Spawning is known to occur throughout the year in some areas (Nishikawa et al. 1985), but regional differences may exist in the peak months of spawning, and the spawning season also varies with skipjack size (Naganuma 1979). Naganuma concluded from analysis of gonosomatic indices (GSI) that peak spawning period for small skipjack tuna (40-60 cm) in the South Pacific is October to December. Argue et al. (1983) examined 11,000 adult skipjack tuna for cannibalism of juveniles (15-70 mm) and for GSI over the same latitude range as this study, but covering 80° of longitude (140°W-140°E). They found that cannibalism and female GSI was highest between October and March in this broad area. More data are needed to identify the regional variation about this general pattern.

The 8 collections of gonads (collections 2-9, Table 1) were treated statistically as 8 "clusters" of random samples of unequal size. The mean proportion of postovulatory follicles <24 h old was calculated as the total number of females with such follicles divided by the total number of mature females. Cochran (1977) pointed out that estimation of variance by the simple binomial probability formula can produce serious errors. The variance was calculated by the appropriate formula recommended by Cochran (1977).

TABLE 1.—Characteristics of 9 collections of female skipjack tuna taken in the South Pacific in 1984.

Collection number	Date	Time of day (h)	*N*	Fork length		Gear[1]	Lat.[2] S	Long.[2] E
				Mean (cm)	Range (cm)			
1	2-23-84	0800	12	47	44-51	PL	23.00	167.00
2	10-20-84	0745	7	49	46-50	PS	16.	178-179
3	10-23-84	0700	6	48	46-52	PS	16.	178-179
4	10-24-84	0700	8	49	46-52	PS	16.	178-179
5	10-25-84	0700	7	50	47-52	PS	16.	178-179
6	10-26-84	0700	14	49	45-51	PS	16.	178-179
7	10-27-84	0645	8	48	46-50	PS	16.	178-179
8	11-19-84	0755	25	50	44-62	PS	03.41	144.08
9	11-30-84	1955	12	56	49-60	PS	0.03	147.46

[1] PL = pole and line; PS = purse seine catch of skipjack tuna attracted to either a fish attraction device moored in waters of 350-450 m deep or natural flotsam.

[2] Latitude and longitude given in degrees and minutes when available.

Three female skipjack tuna were spawned in captivity (23°-24°C; June 1985) at the Kewalo Research Facility of the National Marine Fisheries Service using the stress spawning technique of Kaya et al. (1982). One fish (48 cm fork length [FL]) was sacrificed at the time of spawning, another (43.8 cm FL) 12 h later and the third (44 cm FL) 24 h after spawning. The ovaries of these females were used to establish histological criteria for the aging of the postovulatory follicles of the sea-caught females.

Ovaries were preserved in 10% Formalin[3] and embedded in Paraplast. Histological sections were cut at 5-6 μm and stained with Harris hematoxylin followed by eosin-phloxine-B counter stain (H&E).

Histological Classification

To estimate reproductive condition of skipjack tuna, we used two histological classification systems: one for estimating spawning frequency and the other for assessing the likelihood that a female will continue to spawn (atretic state of the ovary). Each ovary was classified histologically according to both systems. These classification systems were developed for northern anchovy, *Engraulis mordax*, by Hunter and Goldberg (1980) and Hunter and Macewicz (1980, 1985a, b) and are used here with a few modifications appropriate to skipjack tuna ovarian structure and their rates of postovulatory follicle resorption. The descriptions of postovulatory follicles of different ages are from the three captive Hawaiian skipjack tuna. As these fish resorbed their postovulatory follicles much more rapidly than did the northern anchovy, we used stages of shorter duration. The atretic classification system remains unchanged, except for a few minor details of histological structure based on our observations of sea-caught fish. We believe that the reproductive interpretations we associate with the atretic classes are meaningful because the oocyte resorption seems to follow a similar sequence of stages in most teleosts (Bretschneider and Duyvene de Wit 1947; Lambert 1970). The rate a skipjack tuna ovary passes from one atretic state to another is not specified and would require an additional study of captive fish. The characteristics of the two classification systems are outlined below.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Spawning Frequency

Hydrated and Migratory Nucleus Stages

Ovaries with many translucent hydrated oocytes (oocytes enlarged by fluid uptake just prior to ovulation) are classified in the hydrated stage. Spawning is considered to be imminent. In northern anchovy, spawning takes place in <12 h after the onset of hydration. No skipjack tuna with hydrated oocytes were taken in our field collections. Female skipjack tuna were taken with ovaries in the migratory nucleus stage. This stage occurs just before the onset of hydration and is characterized by the migration of the nucleus to the animal pole of the oocyte and the beginning of the fusion of its yolk globules (Fig. 1).

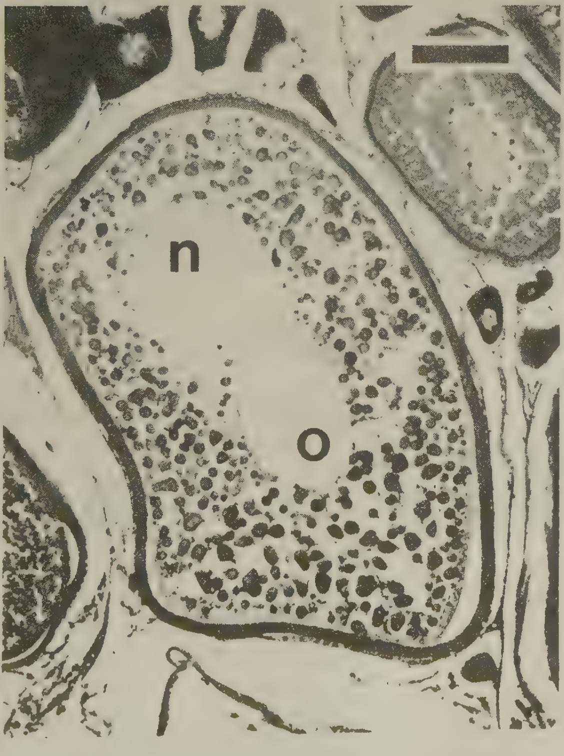

FIGURE 1.—Skipjack tuna oocyte with migratory nucleus (n) and large oil droplet (o); bar = 0.1 mm.

Age 0-H Postovulatory Follicles

Ovaries with new postovulatory follicles with no signs of follicle degeneration are classed as age 0-h postovulatory follicles. Hydrated oocytes may occasionally be present. Estimated elapsed time from spawning is 0-2 h. No skipjack tuna taken at sea were in this stage, but from the laboratory specimen (Fig. 2a, b) we can discern the following histological characteristics: The new postovulatory follicle has an irregular, convoluted shape. The granulosa epithelial cell layer of the follicle appears as an irregularly looped cord of slightly hypertrophied cuboidal cells with prominent healthy nuclei linearly arranged. The granulosa appears only loosely attached to the thecal connective tissue layer. Although the theca is less convoluted than the granulosa layer, it is distinct, contains blood capillaries and appears thicker than the thecal layer seen in northern anchovy.

Age 12-H Postovulatory Follicles

Twelve-hour-old postovulatory follicles (Fig. 2c, d) show signs of degeneration similar to that observed in northern anchovy after about 24 h. Histological characteristics include the follicle which is smaller with fewer convolutions; a lumen which is evident; the degenerating granulosa which is no longer a recognizable unbroken cord of cells, but rather the cells are scattered in clumps in the lumen or may be irregularly attached to the theca; and some pycnotic or irregular nuclei which are evident. The theca has begun to disintegrate although it still remains thick and distinct. Deterioration of the theca is indicated by its overall smaller size, a more filamentous rather than cohesize cellular arrangement, and some irregular nuclei.

Age 24-H Postovulatory Follicles

Ovaries containing 24-h-old postovulatory follicles showed pronounced signs of degeneration similar to that observed in northern anchovy 48 h after spawning. At this stage the follicle is much smaller than that at 12 h but a lumen is still evident (Fig. 2e, f). Only few granulosa cells remain; they usually have pycnotic nuclei and generally are loosely attached to the thecal layer. The thecal layer is still fairly thick although it contains some pycnotic

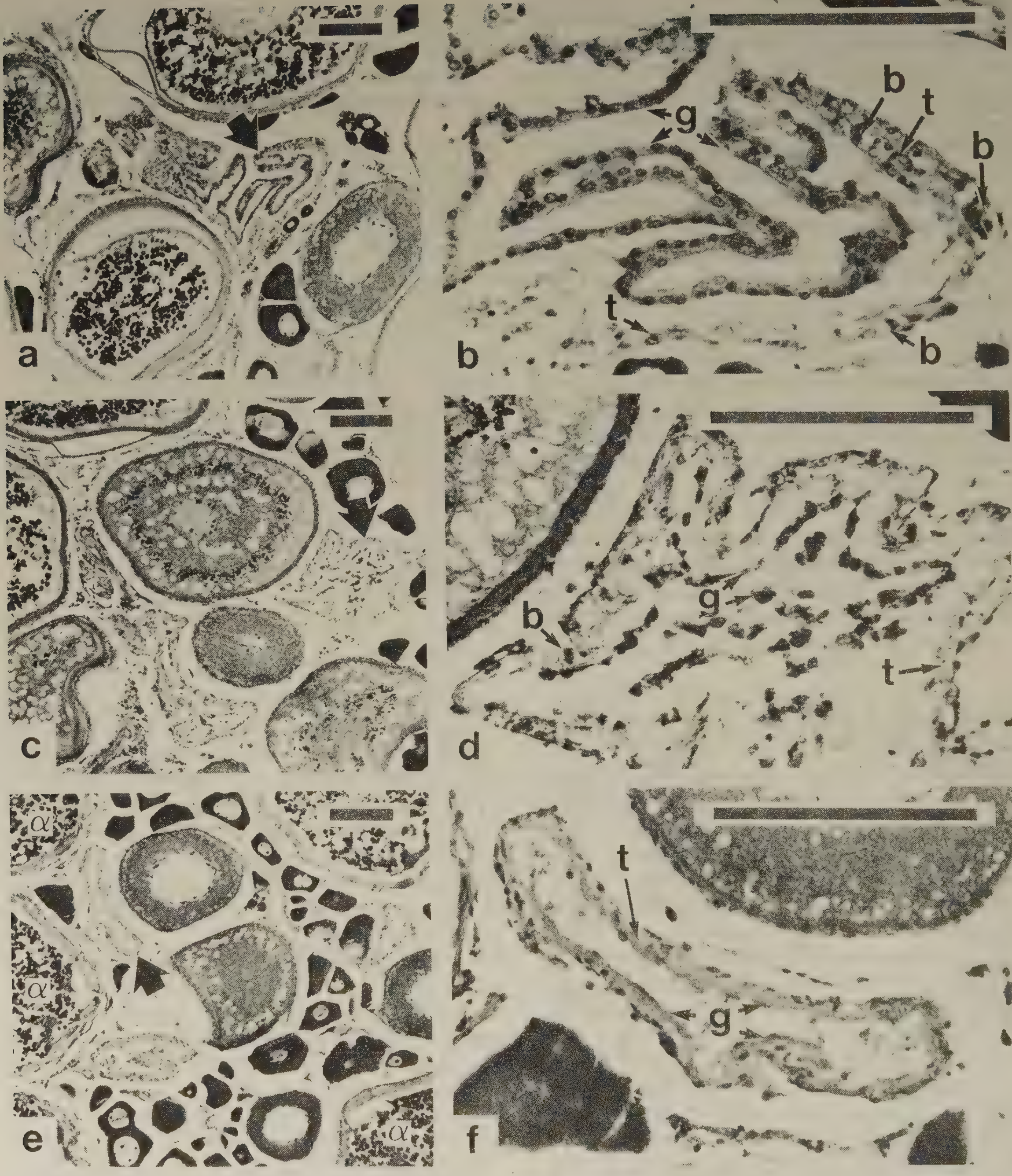

FIGURE 2.—Degeneration of postovulatory follicles of skipjack tuna spawned in the laboratory. Arrow in left panel indicates the postovulatory follicle that is seen under a higher magnification in right panel. a and b, 0 h after spawning (no deterioration); c and d, 12 h after spawning (pronounced degeneration); and e and f, 24 h after spawning (little remains of the degenerating postovulatory follicle). Bar = 0.1 mm; g = granulosa epithelial cell layer; t = thecal cell layer; b = red blood cell(s); and α = early alpha stage atretic oocytes.

nuclei, and lymphocytes, and has a more filamentous composition.

Nonspawning (mature)

Ovaries with many yolked oocytes and containing no hydrated oocytes or postovulatory follicles were classified as nonspawning. They may contain postovulatory follicles in advanced stages of degeneration which cannot be readily distinguished from late stage corpora atretica. Elapsed time from spawning was more than 24 h. Also classified as nonspawning (mature) were females in postspawning condition. The ovaries of such females contained no yolked oocytes, but atretic follicles (beta stage) were present indicating that the ovary was active recently (see next section).

Immature

Ovaries containing no yolked oocytes and no α or β stage atretic structures were classed as immature.

Atretic States

It is well known in seasonal spawning fishes that a low incidence of atresia (resorption of the oocyte and its follicle) occurs throughout the spawning season, but it becomes marked as the spawning season closes and the remaining advanced oocytes in the ovary are resorbed. During the initial atretic phase (α), the oocyte is resorbed and any yolk globules are broken down and resorbed by the hypertrophying granulosa cells of the follicle (Bretschneider and Duyvene de Wit 1947; Lambert 1970). In the next stage (β), all the yolk is gone, and there remains a small, rather compact structure with one or more cavities. The structure is composed of granulosa and theca cells with penetrating blood vessels. Further stages of follicle resorption have been described by the same authors, but the incidence and extent of α and β stages have proven to be the most useful in the classification of atretic states of ovaries (Hunter and Macewicz 1985b). The characteristics of α and β atretic structures are described and illustrated for northern anchovy by Hunter and Macewicz (1985b) and α atretic oocytes of skipjack tuna are essentially similar. However, β atresia differs from northern anchovy in containing numerous spherical vacuoles scattered throughout the follicle. The vacuoles are the remnants of the oil droplet which takes longer than yolk to resorb and in H&E sections appear empty. Occasionally, a large beta stage follicle may be seen in which the granulosa and thecal cells have proliferated.

Listed below are the characteristics of the four atretic states we used to classify skipjack tuna ovaries along with what is known regarding the spawning potential of northern anchovy classed in these states.

Atretic State 0

Yolked oocytes present, with no α atresia of yolked oocytes; β stage atresia may be present, but it cannot be distinguished with certainty from late stage postovulatory follicles (>24 h old). Female northern anchovy in this state have a high potential of spawning.

Atretic State 1

Less than 50% of the yolked oocytes are in the α stage of atresia. The frequency of spawning for northern anchovy classed in this state is less than half of that for females classed in atretic state 0. Thus, atretic state 1 indicates a decline in spawning rate.

Atretic State 2

Fifty percent or more of the yolked oocytes are in the α stage of atresia. The frequency of spawning for female northern anchovy classed in this state is very low and indicates that cessation of spawning is imminent.

Atretic State 3

Ovaries contain β stage atresia and no yolked oocytes. Such fish have completed their spawning season since they have no yolked oocytes. The presence of β stage atresia indicates that oocyte resorption has taken place and thereby distinguishes such recently mature but postspawning fish from immature females. In northern anchovy, atretic state 3 may persist for 30 d.

RESULTS AND DISCUSSION

All postovulatory follicles in sea-caught skipjack were less degenerated than those observed in a laboratory specimen examined 24 h after spawning, indicating that all of those in the sea collections were <24 h old. The fraction of mature females with postovulatory follicles <24 h old ([55 + 18]/86, Table 2) was 0.85 with the standard deviation estimated to

TABLE 2.—Numbers of female skipjack tuna in various spawning and atretic states. The 8 collections taken in the South Pacific between 20 October and 30 November 1984.

Collection number	Atretic state[1]	Age (A) Postovulatory follicles (h)		Non-spawning	Total mature females
		A ⩽ 12	12 < A < 24		
2	0	0	0	2	2
	1	1	0	2	3
	2	0	0	1	1
	3	0	0	1	1
	Total	1	0	6	7
3	0	1	0	1	2
	1	4	0	0	4
	2	0	0	0	0
	3	0	0	0	0
	Total	5	0	1	6
[2]4	0	3	0	0	3
	1	3	0	0	3
	2	1	0	0	1
	3	0	0	0	0
	Total	7	0	0	7
5	0	3	0	0	3
	1	2	0	0	2
	2	1	1	0	2
	3	0	0	0	0
	Total	6	1	0	7
6	0	9	0	0	9
	1	5	0	0	5
	2	0	0	0	0
	3	0	0	0	0
	Total	14	0	0	14
7	0	3	0	0	3
	1	5	0	0	5
	2	0	0	0	0
	3	0	0	0	0
	Total	8	0	0	8
8	0	8	5	0	13
	1	5	2	1	8
	2	[3]1	0	2	3
	3	0	0	1	1
	Total	14	7	4	25
9	0	0	[4]4	[5]2	6
	1	0	[6]6	0	6
	2	0	0	0	0
	3	0	0	0	0
	Total	0	10	2	12
2-9	0	27	9	5	41
	1	25	8	3	36
	2	3	1	3	7
	3	0	0	2	2
	Total	55	18	13	86

[1] Atretic State 0 = no alpha stage atresia of yolked oocytes.
State 1 = alpha stage atresia of yolked oocytes present, but <50% affected.
State 2 = alpha stage atresia present, 50% or more yolked oocytes affected.
State 3 = no yolked oocytes present and beta stage atresia present.

[2] One female skipjack tuna in collection 4 was immature.

[3] A female with hydrated oocytes and age 0 h postovulatory follicles.

[4] Three of these females had oocytes in migratory nucleus stage.

[5] Two of these females had oocytes in migratory nucleus stage.

[6] Five of these females had oocytes in migratory nucleus stage.

be 0.071 (Cochran 1977; see methods). This means that the average interval between spawnings (1/0.85) was only 1.18 d. Only one female was immature, reducing the denominator for the above fraction spawning from 87 to 86. If we consider only those females with yolked oocytes and no or minor atresia (atretic states 0 and 1) the fraction spawning is 0.90, implying a mean interval of 1.11 d between spawnings. This indicates that the spawning rate of female skipjack tuna in prime reproductive condition is very close to daily.

High levels of ovarian atresia were much more common among the 12 females taken in February than those taken in October-November, indicating that the February fish were nearing the end of their spawning season. Females with highly atretic ovaries (state 2) and postspawning ovaries (state 3) constituted 66% of the fish in the February collections (Table 3), but they made up only 10% of the fish taken in October-November. The February collection was the only one taken by pole and line. It is possible that pole-and-line fishing may be selective against spawning fish (Iverson et al. 1970; Matsumoto et al. 1984) although some spawning fish were taken in this collection.

The most unusual feature of the February collection was that the spawning fraction was high, 0.25 for a group where 50% of the fish were in postspawning condition, had no yolked oocytes, and were incapable of spawning (atretic state 3). The spawning fraction was 1.0 for the three females with no or minor atresia because all three had postovulatory follicles. Thus skipjack tuna with active ovaries appear to spawn nearly every day. It appears that those unable to maintain this rate may discontinue spawning and resorb the ovary because females with active ovaries, showing no evidence of spawning, were rare in all collections. Postspawning females

TABLE 3.—Numbers of female skipjack tuna in various spawning and atretic states. This single collection was taken 23 February 1984.

Collection number	Atretic state[1]	Postovulatory follicles		Non-spawning	Total mature females
		12 h	24 h		
1	0	2	0	0	2
	1	1	0	1	2
	2	0	0	2	2
	3	0	0	6	6
	Total	3	0	9	12

[1] Atretic State 0 = no alpha stage atresia of yolked oocytes.
State 1 = alpha stage atresia of yolked oocytes present, but <50% affected.
State 2 = alpha stage atresia present, 50% or more yolked oocytes affected.
State 3 = no yolked oocytes present and beta stage atresia present.

might reactivate their ovary sometime later in the year if their physiological condition favored reproduction. Evidence for northern anchovy indicates that the transitions from spawning to postspawning states and vice versa can occur rapidly. In the laboratory at 16°C, northern anchovy can resorb all advanced oocytes within a few weeks (Hunter and Macewicz 1985b) and can produce an active ovary in 30 d (Hunter and Leong 1981). Owing to the higher water temperatures and high metabolism of skipjack tuna they are probably capable of even faster reproductive cycling.

Histological examination of females taken late in the day (1955 h, collection 9) provided additional evidence for daily spawning. Eight of 10 females with postovulatory follicles in this collection also had oocytes in the migratory nucleus stage. This stage is the precursor to hydration. Thus, fish which had spawned <24 h before were beginning to hydrate a new batch of eggs which presumably would be spawned in <12 h. The migratory nucleus stage was observed only in this collection probably because it was the only one taken in the evening, whereas all others were taken in the morning (0645-0755). The rarity of females with hydrated oocytes in our collections and the age of the postovulatory follicles imply that spawning usually took place at night. Spawning in daylight hours has been observed by fishermen and scientists, however (Iverson et al. 1970; Matsumoto et al. 1984).

A single female taken during the morning (collection 8) had small (0.70 mm) early stage hydrated oocytes (hydrated oocytes in which the yolk globules had not fully fused). This female, the only one with hydrated oocytes in our collections, also had new postovulatory follicles despite the fact that the hydrated oocytes were not fully advanced. This female may have been induced to hydrate and spawn by the stress of capture or may be simply an exception to the rule. To capture significant numbers of females with hydrated oocytes would probably require sampling after 2100 h. It is important to capture eventually some females in the hydrated stage because it is the best way to confirm that all oocytes in the most advanced modal group, the group of oocytes considered to be the next spawning batch (Hunter and Goldberg 1980), are in fact spawned. Counts of hydrated eggs are also the easiest and most accurate method of estimating batch fecundity (Hunter et al. 1985).

The "stress" spawning technique of Kaya et al. (1982) was used to produce the spawned skipjack tuna for the aging of postovulatory follicles. In this technique females captured at sea and placed in a tank spawn spontaneously, usually about 8 h after capture presumably because of the stress of capture and handling. Spawning typically takes place at about 2400 h, which, by our estimate, appears to be close to the usual time of spawning. It now seems likely that many of these fish are naturally expressing their daily spawning activity. On the other hand, eggs less than the normal size range, 0.8-1.17 mm (Matsumoto et al. 1984), are occasionally spawned, indicating that stress may induce premature hydration in some individuals. That the skipjack tuna do not continue to spawn in the tanks is due probably to the stress of captivity. Our examination of a captive skipjack 24 h after spawning indicated that nearly all remaining oocytes containing yolk were in the early stages of alpha atresia (Fig. 2e). Similarly, female northern anchovy nearly always resorb their advanced oocytes a few days after capture although they will subsequently mature and spawn (Leong 1971; Hunter and Macewicz 1985b).

If female skipjack tuna spawn at the frequency we observed (85% of the females per day), the cost of reproduction and annual fecundity will be high because skipjack tuna appear to have a long spawning season. The relative batch fecundity of skipjack (number of eggs per spawning per body weight) is about 100 eggs per gram (Matsumoto et al. 1984; Goldberg and Au 1985). Skipjack tuna eggs are about the same size as those of *Scomber japonicus* which average in weight 0.04 mg (unpubl. data, National Marine Fisheries Service, Southwest Fisheries Center). We estimate the cost of a single spawning (excluding the metabolic cost of egg maturation and reproductive behavior) to be about 2% of the body weight per spawning (*Scomber* egg dry weight × relative batch fecundity × conversion to wet weight; $4 \times 10^{-5} \times 100 \times 5 = 0.02$). If a female spawned every 1.18 d over 3 mo (90 d), it would produce about 7,600 eggs per gram body weight at an average daily cost of 1.7% of the body weight per day; a 4 kg skipjack tuna would spawn about 30 million eggs over this period.

If the collections used in this study were an unbiased sample of the South Pacific skipjack tuna population, then little doubt exists that spawning occurs almost daily when they have active ovaries. This preliminary study provides the tools necessary for a population-wide assessment of reproduction. We established the time-specific, histological criteria for assessment of spawning rate, and the method was applied to a small sample. A great deal more remains to be done for a proper assessment of reproduction in skipjack tuna. Specifically, many more samples at different times of day, using a variety of fishing gears, are needed to insure that sampling biases do not exist; a wide range of skipjack tuna sizes or ages need to be sampled so that the age-specific reproductive effort can be estimated; and females with hydrated oocytes need to be collected to verify that nearly all oocytes in the most advanced mode are hydrated and spawned. The last point seems particularly important because our estimated body weight cost of reproduction is high and is very sensitive to the estimate of batch fecundity. It may never be practical to analyze histologically sufficient numbers of specimens to estimate spawning frequency for all months and ages since some spawning occurs the year around (Nishikawa et al. 1985). On the other hand, it may be practical to calibrate the gonosomatic index (GSI) in peak spawning months using histological criteria and to use the GSI as a calibrated index of spawning frequency during months of low spawning frequency. We do not intend to continue this work but we encourage those working on the biology of tunas to include such studies in their research plans.

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A PRIMER ON LIMITED ACCESS ALTERNATIVES
FOR THE PACIFIC COAST GROUNDFISH FISHERY

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PREFACE

The commercial groundfish fishery off the Pacific coast grew rapidly between 1976 and 1982. Annual shoreside landings more than doubled, the foreign trawl fishery dwindled to almost nothing, and the "joint venture" fishery was born and prospered. To accomplish this growth in landings the groundfish trawl fleet expanded from less than 300 to over 440 vessels. Economic conditions, however, proved incapable of sustaining the growing fleet of new, modern trawlers. Neither the Pacific coast rockfish stocks nor the traditional flatfish and sablefish stocks provided the needed room for expansion; nor did the Alaska groundfish fishery absorb the new vessels quickly enough. Economic returns to trawl vessel operators, especially those with big mortgage loans on new vessels, fell below levels needed to justify the investments. Many vessels failed financially, and lenders began repossessing vessels from owners with delinquent loans.

During 1982 the Pacific Fishery Management Council was petitioned by a small group of trawl fishermen to adopt an "immediate emergency moratorium on all groundfish trawling". Also, both the Council's groundfish management team and Scientific and Statistical Committee noted that limiting entry to the fishery should be considered as a management tool. In the fall of 1984 the Fishermen's Marketing Association in California and the Coast Dragger's Association in Washington state jointly proposed that each of the Pacific coast states create a trawl vessel license and place a moratorium on issuing new licenses. When draft legislation failed to gain sufficient support in Oregon, the moratorium effort lost momentum. Movement toward limiting entry to the groundfish fishery ground to a halt when the Pacific Fishery Management Council voted not to consider a limited entry system for groundfish during its groundfish plan amendment process in 1985.

In 1986 economic conditions in the trawl fishery have improved due to a resurgence in the pink shrimp fishery, the reduced number of vessels in the fleet, and the lower capital costs faced by purchasers of distress-sale vessels. Although fishery management agencies are not now considering a limited access program for groundfish, the Council and the Pacific coast states may be faced with making such a decision in the future. Access limitation does afford fishery managers several benefits not achievable with traditional fishery regulations. In the first chapter below, nine objectives of limiting access are listed. Among these objectives are economic efficiency, reduced management costs, increased and stabilized fishing fleet profits, equitable distribution of fishery economic benefits, and reduced burden of regulations on the industry. While the reasons for limited access focus on social and economic aspects, it may also contribute to fish stock conservation.

To prepare a thorough examination of alternative approaches to limited access for use in future discussions, a Working Group on Limited Access was formed in November of 1984. The Working Group consisted of economists and fishery management personnel from the National Marine Fisheries Service, Pacific Fishery Management Council and Oregon State University. The attached material is taken from two chapters of that group's extensive report.

The Working Group was assisted by an advisory committee, organized by Ed Ueber of the Southwest Fisheries Center, called the Groundfish Alternatives Management group (known as the "GAM"). This group included a representative from each of the three coastal state's fishery management agencies, and several private industry people. The GAM reviewed drafts of the Working Group's report, and provided comments and suggestions during three meetings spaced over a 14-month period. Members of the GAM are not necessarily in agreement with particular conclusions or views expressed in the final report. Nevertheless, their thorough criticism of earlier draft reports and their frank and open expression of viewpoints helped immeasurably to improve the final report. This summary report is a response to one of the GAM's suggestions. We hope that it proves useful to those members of the public that are concerned about the future direction of fisheries management and want to do something about it.

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INTRODUCTION -- LIMITED ACCESS, WHAT IS IT AND WHY?

Despite its wide acceptance in other fisheries, limited access remains a controversial topic among Pacific coast groundfish fishermen and fishery managers. It is controversial because it immediately opens a wide array of public policy issues. How should the public conserve fish stocks, and who should benefit from harvesting those fish? What are the costs and benefits to the public, the taxpayer, the fishing industry, and the coastal communities supporting the groundfish industry? Should the government push the industry to be economically efficient in harvesting, or should it discourage technical efficiency to conserve stocks? Should management policy preserve the economic status quo by protecting existing harvest shares? These are some broad issues occupying the discussions of policy-makers and academic writers concerned with resource management.

The goal of this introductory section is to define limited access, to dispel some basic misunderstandings about limited access, to clarify the optional forms of limited access, and to review the various resource management objectives addressed. This should set the stage for the following, more lengthy discussions. By reducing the scope of needless misunderstandings, it should also help to make future discussions of limited access more productive.

WHAT IS LIMITED ACCESS?

Limiting access in commercial fisheries is commonly implemented through either license limitation or assignment of quantitative harvest rights. License limitation, most commonly known as "limited entry", is the simplest and most widely used form of limited access in the United States.

A license limitation system issues permits to specific individuals (usually fishermen or fishing vessel owners) and prohibits landings by those not having a license. As will be explained at length below, licenses can be annually renewable or perpetual fishing rights; they may be openly tradeable or strictly assigned to a particular person; they may be specific to a gear type or species of fish. A wide range of conditions and limitations can be placed upon the exercise of fishing privileges bestowed through issuance of a license.

Rather than simply identifying who can fish, quantitative harvest rights designate how much each permittee can take. Like license limitation, a quantitative harvest rights system can take on a number of different characteristics. A variety of terms have been coined for the various quantitative harvest rights schemes. These include (1) individual fisherman quotas, based upon Francis Christy's original proposal in 1973, (2) individual tradeable quotas, as recently adopted in New Zealand (I.N. Clark and A.J. Duncan, 1986), (3) quota licenses as proposed by Canada's Commission on Pacific Fisheries Policy (Peter Pearse, 1982), and (4) quota shares or allocated vessel quotas (C. Clark, 1980) which represent individual shares of total allowable catch. Throughout most of the discussion we will use the term "individual fisherman quota" (IFQ), recognizing that individual quotas may be allocated to vessel owners or fishing enterprises rather than to fishermen. Regardless of what term is used, a quantitative harvest rights system controls the total harvest by distributing harvest shares among participants in the fishery.

To some degree all fishery regulations dictate the conditions under which fishermen are allowed access to fish stocks. Traditional forms of fishery regulations -- including harvest quotas with season closures, gear requirements, size limits, and trip limits -- restrict access to fish stocks. This is an inherent part of defining terms and conditions for legal resource use. To control annual harvests, these regulations must reduce the level of fishing effort from what it would be without regulation. Hence, all fishery conservation regulations, both traditional and limited access, conserve fish stocks by controlling the level of fishing effort, and this requires placing limits on the use of stocks.

What then is the essential difference between a limited access system and the traditional approach to fishery regulation? The main difference is that traditional regulations seek todirectly control harvest levels without saying who should be allowed to take a portion of the total allowable harvest, while limited access begins by identifying who is permitted to harvest and, possibly, how much they are allowed to harvest.

Limited access does not completely replace the need for traditional regulations. License limitation, for example, does not directly control the level of harvest by license-holders. Consequently, it may need to be supplemented by fishery-wide quotas and technical restrictions on vessels and gear. Similarly, even though an individual quota system inherently controls total harvest, additional regulations may be needed to achieve optimal utilization of the fish stocks. This is especially true in multi-species, multi-gear fisheries. Recent experience indicates that individual quotas, by themselves, do not provide sufficient control of size-at-capture, incidental catches, and discards.

Limited access may exist without government regulation. Where the law (or tradition) recognizes an individual's right to portions of a resource, such as in the famous Maine "lobster fiefs" (Acheson, 1975), limited access may operate without formal sanction. Private rights to land, forests, and other forms of private property impose similar forms of limited access and controlled use. The point is that access to the resource for harvesting purposes is limited to some identifiable set of people. Where legally defined rights exist, the owners of these rights may sell, trade and bequeath the rights to others. Thus the identity of the users may change over time. Access to the resource is limited to those who possess use rights; but, in a commercial sense, the resource is open to all those who obtain use rights by paying the market price or by complying with state-imposed qualifications.

A limited license or an individual quota does not represent a right that is as respected and reliable as a registered deed to land. Both licenses and individual fisherman quotas (IFQ's) represent use rights, not property rights to the fish stock. In the legal jargon these are termed "usufructuary rights", meaning rights to use and enjoy the fruits of property not belonging to the individual. The fish stock in the ocean remains a public resource to be managed by the state as a public trust. However, when licenses and IFQ's are marketable they take on many of the characteristics of property, including a market price. Because these limited rights are the creation of administrative decisions, they may be revised and amended by further administrative action.

WHY USE LIMITED ACCESS? WHAT IS DIFFERENT ABOUT FISHING?

Commercial fishing differs from farming, small-scale retailing and other competitive American industries in many respects; the most important is the lack of private property rights in the essential resource. Unlike farm land and mineral deposits, marine fish populations are not owned by the users. Historically, in western Europe and North America property rights to marine fish stocks did not evolve along with rights to land-based resources. There are two principal reasons for this. First, it was not until the rapid expansion in world fishing after the World War II that conservation of marine fish stocks was recognized as a serious and widespread problem. So long as people believed in the inexhaustibility of marine fish, there was little need to develop institutions for limiting access to fisheries. Second, creation and enforcement of rights to marine fish are difficult tasks. Fish are not easily observed and fenced like a plot of land. To establish, enforce and exchange property rights in fish requires the establishment of new and expensive institutions.

In the United States marine fish stocks are either open access or common property resources. An open access resource can be accessed and harvested by anyone. There are no restrictions on who can harvest or upon individual harvest levels. An open access resource is literally no one's property (not strictly property at all). Most Pacific coast groundfish stocks are open access resources. In contrast, access to and use of a common property resource is restricted to an identifiable group of owners having co-equal use rights. The original common lands of a medieval village, for example, were used in common by members of the village owning the land. Others were excluded from using the commons. (See Ciriacy-Wantrup and Bishop, 1975.)

A license limitation system converts an open access resource into a kind of common property resource. Although the licensed fishermen are not legal owners, they are a known and exclusive group with co-equal harvest rights. With either open access or common property, competitive free enterprise among resource users cannot be expected to assure adequate resource conservation. Group restrictions on annual harvests are needed. This need has long been recognized, and it is the reason that public management of fisheries is so common.

Collective management actions are needed for a very simple reason: economic incentives of individual fishermen rarely favor conservation. In an open access or common property fishery the fishermen may not directly sense the resource depleting effect of their own actions. Even if a fishermen does notice the effect his harvest has on the fish population, he will not restrict his harvest unless he expects to receive some future benefit from doing so. If there are others fishing on the same stock, one individual's benefit from his conservation action depends on others acting in concert. Without assurance of collective action, a fisherman's sacrifice for the sake of conservation may simply create benefits for those not restricting their harvests. Also, without limited access, increased resource abundance may attract new entrants who dilute the economic benefits of conservation available to established resource users.

Thus individual actions, based upon self-interest, cannot assure adequate conservation and cannot effectively promote long-term economic returns from a common property natural resource. However, fishermen will all gain from appropriate collective restrictions on use. Collective action is also needed to properly conserve groundwater basins and public grazing lands. Restrictions on individual resource use can be adopted through cooperative agreements among users, through certain regional resource agencies like water districts, or even through Federal regulations. In all cases optimum management requires that individual incentives for short-term economic gain be brought into line with sustainable levels of use.

Regulation of common water supplies and grazing lands normally involves quantitative limits to individual use. In medieval England many villages had commons which were regulated through "stinting" -- a term for limiting the number animals grazed by individual peasants. Similarly, sheep and cattle ranchers using public grazing lands in the western U.S. are allocated so many "animal unit months" (AUM's) which roughly corresponds to a known quantity of forage harvested. Farmers irrigating fields in Central California each have a quantity of water to which they are entitled. This entitlement may be attached to the land as a "water right". These water and grazing rights are actually a form of limited access, because they designate both (1) which individuals have use rights and (2) the amount of use allowed.

Note that these forms of limited access are not intended to prevent people from becoming farmers or cattlemen. There is no list of licensed or "qualified" farmers. If you want to try your hand at raising almonds in Kern county, you can buy or rent land and obtain the necessary water rights. There is unrestricted entry to the industry. Fishing, farming and retailing are similar in this important respect. To exercise this right of entry, a business firm must acquire the necessary implements and materials. In farming or ranching one requirement is a source of water or range land forage. In an open access fishery, however, a new entrant cannot acquire rights to a given quantity of fish. A newcomer simply dips into the common pool, often taking a portion of the available harvest away from established fishermen.

Rather than limiting the number of harvesters, groundfish managers have established aggregate harvest quotas (or guidelines), and have instituted other restrictive rules on fishing enterprises in order to achieve economic and social objectives. Individual fishing firms then compete for fish based upon harvesting capacity and skill. When quotas are inappropriate, managers may prefer to restrict effectiveness of the gear (such as maximum allowable length of gill nets) or the portion of the stock that is vulnerable to harvest (mesh size regulations, for example). Pacific coast groundfish regulations incorporate many of these methods. While these harvest regulations may adequately prevent fish stock depletion, they do not address a number of other problems.

Economic and social problems frequently occur in quota-regulated open access fisheries. Some of these problems are:

(1) Economic profits are lost to increased fishing costs. Because individual fishermen can maintain or expand their individual harvest shares only by catching more fish, they compete by increasing fishing capacity. Despite the increased costs involved, the individual vessel owner may enjoy increased earnings. When the fish stocks are under quotas, increased fishing capacity results in no increased fish catch but does raise the total cost of taking the quota.

(2) Over-crowding and gear conflicts occur. Fishermen concentrate in the best fishing areas and during the best fishing seasons. In some cases this results in a very short and furious fishing season which may pressure individual fishermen to operate under less safe conditions. This can cause loss of gear and can increase the cost and risk in operating a fishing vessel.

(3) Economic instability is increased. Excessive numbers of new entrants are often attracted to fisheries during periods of higher-than-normal profits. Many of these new firms will go bankrupt under normal circumstances, leaving the fishing fleet over-built and with many financially-strapped firms. While cyclical instability affects many industries, this is amplified in quota-regulated commercial fisheries by changing harvest regulations. When new vessels swarm into a fishery during good years, managers tighten the harvest regulations in response.

(4) With large amounts of redundant harvesting capacity regulatory burdens and management costs become excessive. To assure adequate fish stock conservation, there must be restrictive fishing regulations. Annual quotas may be augmented by trip limits and other restrictions. To implement regulations there must many committees, hearings, and enforcement agents.

Limited access to commercial fisheries is in part a response to these social and economic issues, but it may also be used as a resource conservation tool in fisheries that are less heavily exploited. Some Australian limited access programs, for example, were adopted early enough in the developing fishery to provide a substantial measure of protection to the resources.

OTHER APPROACHES TO ECONOMIC REGULATION OF FISHERIES

It should be noted that the license limitation and IFQs are not the only alternative approaches to common property resource management currently under serious discussion. A radically different approach would be to levy taxes or royalties on fish landings. This sort of approach has been given serious consideration in designing programs to reduce air and water pollution (e.g. the so-called "pollution taxes"), and public interest groups have touted proposals to increase charges for irrigation water and public grazing lands where those resources appear to be over-used or misused. The basic logic of a tax charge is that it changes economic incentives in the correct direction.

Firms using common property resources and firms relying on publicly subsidized resource development projects, do not bear, nor do they adequately take into consideration, the full cost of resource use. This is related to lack of private property rights. The fishing firm does not have a direct financial interest in the economic value of the fish stock, its only interest is in the share of the stock that it can capture and sell. Consequently, the cost of reducing the fish stock (i.e. reduced catch rates for all firms and reduced future availability of fish) is not felt directly by the firm and it does not consider that cost in deciding how much to harvest. A rancher, on the other hand, must account for the effects of a reduced herd on the book value of his livestock. Similarly, a hypothetical private fish stock owner would bear the cost of a reduction in his fish stock. The prospect of a reduced asset value associated with overfishing would act as a strong incentive to harvest at an economically efficient level. Since firms fishing on a common property stock do not experience the reduced asset value they do not have the proper incentives to conserve. One solution is for a public agency to compute the cost associated with reduced fish stock size and to levy a royalty fee equal to that cost. After that, the private firms should lose any incentive to overfish.

This proposal has been described in textbooks and academic papers, but has never been applied to a fishery. There are several good reasons why this has not been adopted elsewhere, and these reasons apply equally to the case of Pacific coast groundfish. First, fishery decision-making is strongly geared to protecting the rights and financial interests of current resource users. Since the harvest royalty would appear to reduce the income of fishermen, it would work to the disadvantage of exactly those resource users who are most clearly represented in the political process. Also, if the fishing industry is suffering economic strife it may be considered grossly unfair to impose additional taxes. These political and equity aspects raise strong objections to using royalties as a resource management tool.

Other practical reasons for not using landings taxes to manage fish stocks are (1) that computational task is extremely formidable, and (2) the necessary flexibility in levels of taxation is not suited to our legislative system. Because the royalty or tax should equal the cost associated with reduced asset value of the fish stock, the tax would have to be adjusted as fish prices, fishing costs and fish stock abundances change. Given the imprecision in fish stock assessments and the frequency of changes in prices, it is unlikely that the tax rates could be accurately computed and adjusted. Also, authority to set tax and royalty rates is not now delegated to state fish and game agencies or to the Pacific Fishery Management Council. Thus the legislatures would have to change tax rates in a timely and appropriate fashion. This is not a likely prospect.

OBJECTIVES OF LIMITING ACCESS

Limiting access to commercial fisheries can address many different objectives. Some of the more prominent objectives are as follows:

1. To promote economic efficiency in harvesting.
2. To establish stable and secure tenure to the fishery for licensed fishermen.
3. To enhance the value of fishery products delivered to consumers.
4. To increase and stabilize the profitability of the fishing fleet.
5. To reduce the burden of management regulations on the industry.
6. To reduce the cost of fisheries management born by the public.
7. To secure an equitable distribution of benefits from the fishery.
8. To protect various segments of the fishing industry from other fishermen and non-commercial interests.
9. To help restrain fishing effort and conserve fish stocks.

This list does not include every conceivable objective, but it does illustrate the broad range of considerations that can be addressed. A brief explanation of these objectives will focus the later discussion.

Economic efficiency in harvesting requires delivering the available raw fish to dockside with the least possible cost expended on fishing and delivering the fish in appropriate condition and on a time schedule suitable for marketing. Because open access fisheries normally exhibit substantial excess fishing capacity, which is controlled by quotas and other economically inefficient regulations, substantial advances may be made toward this goal through limited access. To actually calculate an efficient harvest program is a difficult task that is rarely attempted. Huppert and Squires (1986) recently estimated that an efficiently operated Pacific coast groundfish fishery could generate between $7 million and $17 million annually in net economic profits. The precise level of potential profit depends largely on the joint venture whiting fishery and the pink shrimp fishery. The best estimate is $12 million profit, and this would require a reduction in fishing fleet size of about 40 percent in the fleet operated in 1984. Without limited access, the free entry of fishing vessels tends to dissipate these potential harvesting profits. A new limited access system may not be able to achieve the estimated level of economic gains in the short run, because it would be saddled with a large existing fleet. Nonetheless, the potential gains are sufficient to make increased economic efficiency an important objective.

Secure tenure in the fishery has at least two dimensions. With secure tenure a fisherman would not have meet some state-imposed performance standard in order to continue in the fishery. It also means that a fisherman is assured of future benefits from sacrifices made to conserve fish stocks. In open access fisheries, and in some license limited fisheries, a fisherman cannot reduce his fishing or stop fishing temporarily in hopes of harvesting larger or more numerous fish later. With secure, individual fishing rights, however, a fisherman can afford to fish more slowly and to wait until fish are of optimal size or in optimum condition.

The quality and timing of fish delivered to market may be improved under a limited access system. Fishermen and processors operating under open access are sometimes forced to compete for fish by harvesting in a hurry. This may result in increased occurrence of spoiled or unnecessarily frozen fish products. This is especially a problem when traditional quota management results in short fishing seasons that overwhelm the processing and distribution sectors. If fishermen are given individual quotas, they are free to stretch out the fishing over a longer period of time. Recent Pacific halibut experience provides the classic example of open access fishing causing so short and furious a fishing season that the extraordinary efforts are needed to assure product quality maintenance and almost all the fish have to be frozen.

Profits are usually high when fishing fleets begin exploiting a new fish stock or have a particularly large year-class of traditional fish stocks. The usual tendency, however, is for profits to fall as additional vessels are attracted. If the fleet size grows as the fish stock is depleted, then a period of serious economic dislocation will ensue. Recent experience with rockfish stocks off the Pacific coast provides a case study in this process. A properly managed limited access system should be able to reduce the instability in profits by attenuating the growth and decline in the fishing fleet. Higher fleet profits can be earned when the numbers of fishing vessels is just sufficient to harvest the available yield. Sustained high profits require stability in market prices, costs, and fish stocks. Limited access cannot provide stability in all these, but it does remove one common source of economic instability and should result in higher average annual profits.

Reducing the burden of fishing regulations on the industry is an appropriate goal, but it is unclear what particular change in regulations constitutes a reduced burden. Regulations on gear quantity or design, commercial fishing seasons, and "trips limits" may be viewed as a burden. From an economics perspective, all these forms of regulation cause private fishing operators to incur additional costs. By establishing a reduced and more efficient fishing fleet, limited access may permit some of the regulations to be removed. Whether such a change would result in an overall reduction in burden of regulations is largely a matter of definition and perception.

Reducing the public expenditures on management would relieve the taxpayer's burden of fishery regulations. The current groundfish management system uses public resources to perform necessary biological research and fish stock assessments, to monitor fish landings, to support Coast Guard and State marine enforcement operations, to carry out legal sanctions against violators of regulations, and to make public decisions on management plans. A recent rough estimate of costs associated with Pacific coast groundfish indicates that about $4.5 million is spent on resource assessment, and $5.6 million on management, enforcement, coordination and communications. Costs of managing a fishery will, of course, depend partly upon the character of the fishery and partly upon the types of regulations promulgated. If limited access is conducive to lower management costs, this should be an important consideration.

Everyone agrees that fishing regulations should entail an "equitable" distribution of benefits. Although there is no widely recognized definition of equity, there are clear patterns in management practice. In a recent study of twelve government programs that allocate property rights, Elizabeth Rolph (1983) found that policymakers deal with the equity issue by designing regulations to minimize any redistribution of wealth. Where established resource users enjoy benefits of a communal resource (such as in land development, air pollution, groundwater pumping) "the judicial, the legislative, and the executive branches have uniformly supported the claims of historic users when allocating rights". This principle seems to be honored by existing fishery limited access systems as well. A reasonable way of dealing with the equity question, therefore, may be to assure that no established fishermen suffer a measurable loss due to the access regulations. As a first approximation this can be accomplished by retaining historic allocations of catch among existing gear types, vessel size classes, and geographic sub-divisions. However, if rapid changes have been occurring in the fishery, it is not clear that historic shares provide an equitable solution. New entrants and previous operators with new vessels may claim a right to increased shares. Nevertheless, initial preservation of historic catch shares under a limited access system provides one simple and operational means of dealing with the equity issue.

To protect various segments of the fishery from one another may be more than just another form of the equity issue. Where recreational or environmental interests collide with commercial fishing interests, a limit to commercial fleet size may help to quell strong political and economic forces that could eliminate the fishery entirely. California has adopted license limitation programs in the swordfish and shark drift gill net fishery and in the northern California set gill and trammel net fishery in order to deal with politically potent rivalries between user groups (Huppert and Odemar, 1986). Limited access has proved to be a useful tool for staking out territories and limiting the range of conflict.

Finally, limited entry can assist in conserving fish stocks. In the case of license limitation, the control over fishing effort may be too weak and ineffectual to assure fish stock conservation. On the other hand, an individual quota system provides direct controls over total harvests and may be a useful substitute for other forms of effort regulation.

No single system of regulation could address all nine of these objectives simultaneously and with equal success. A limited access system must be tailored to the specific objectives sought. And it must address the various private and public interests reflected in the objectives discussed here.

CONCLUSIONS

Several conclusions from the preceding discussion are worth repeating and summarizing. First, a limited access system is basically a social mechanism for reducing the excessive competition for fish that occurs when fish stocks are open to all comers. It is an alternative or a complement to traditional quota, season and gear regulations. Among the alternative regulatory systems, it is uniquely able to address economic efficiency of the commercial fishing industry. In fisheries that are already highly regulated like Pacific groundfish, limited entry should be viewed as one component of a multi-dimensional management strategy. The choice is not between limiting access to the fishery or having a free and open commercial fishery. Rather it is between one set of regulations on competitive fishing and another set.

Second, there are several kinds of limited access. The two alternatives receiving the most attention are license limitation and IFQs. With either major type of limited access there are numerous variations in detailed application. Much public discussion and participation should be devoted to determining exactly what features to include in a limited access program for any particular fishery. The ultimate allocation of benefits from the fishery would depend upon the detailed decisions made in designing an actual limited access program.

Third, the problems of economic competition for common property or open access resources are not unique to fisheries; adoption of limited access rules are implicit in many other economic systems, including that of private property resource ownership. Rules for use of range land, groundwater supplies, and the air have similar features to fishery regulations. While the elusive marine fish populations are not susceptible to subdivision into pieces of private property, the limited access approach attempts to generate some of the conservation and economic benefits that flow from a free enterprise, private property system.

Finally, although it has not been explicitly stated, it should be clear to the reader that selection of fishery management methods determines what fishing rights or privileges, with corresponding economic benefits, the community bestows upon commercial users of the fishery resource. When a season closure or a license limitation is adopted by the fishery management authorities, the fisherman's economic gain from fishing is altered. Thus it is clear that the nature of fishing rights or privileges are subject to change at the discretion of fishery councils. Commercial fishing rights are not "inalienable rights" like the right to free speech. They are even less secure from political meddling than standard property rights applying to one's personal possessions. To the extent that a limited access system does establish broader and more secure fishing rights, it will place the fisherman in a position much closer to that of a property owner. But the key decisions will remain those of the public managers whose trust responsibility is established by the various state and federal laws.

BASIC ELEMENTS OF A LIMITED ACCESS PROGRAM

This section presents the basic "nuts and bolts" of limited access, and carries the discussion of limited entry beyond the general considerations reviewed in the previous sections to look at specific elements. A proposed checklist of items for consideration, along with a brief description of the main options is presented in Table 1 below. Seven basic decision categories are:

(1) Scope of the fishing activity to be restricted or allocated,
(2) Method of limiting access,
(3) Initial allocation of harvest rights,
(4) Transferability of harvest rights,
(5) Longevity of harvest rights,
(6) Mechanisms for adjusting the number of harvest rights,
(7) Handling disputes regarding issuance and transfer of rights.

The discussion of these seven elements will focus on Table 1 and the trawl license limitation proposal developed by the Fisherman's Marketing Association and Coast Draggers Association in 1984 (Attachment 1). Although that proposal was called a moratorium, it has the essential features of a license limitation program. Of interest here is the contrast between the features outlined in that specific proposal and the alternatives listed in Table 1. The seven categories are discussed in order.

SCOPE

The FMA/CDA proposal envisions a relatively narrow scope for the license limitation program in some respects (limited to trawl vessels) and a rather broad scope in other respects (covers entire coast and all species of groundfish listed in the Management Plan). It leaves out all other commercial gear types and recreational fishing. Except in southern California, the recreational component of groundfish catch is too small (and will probably remain too small) for this exemption to matter much. Ignoring other gear types, however, is a more substantive deletion. Although trawl gear dominates the total catch, traps and longlines take a substantial amount of some species, and gill net fishing has grown to significant proportions in California. One strength of trawl-only approach is that it limits the most important element of the commercial fleet while minimizing the number of individual fishing operations that must be regulated.

By including all groundfish species and all fishing sites on the West coast, the FMA/CDA proposal would preserve great latitude in trawl fishing operations. Trawl vessel operators have suggested that they need to have many options open to them under any regulatory system. Geographic area and fish species are important dimensions of operational flexibility. Trawlers may move seasonally from northern to southern ports, they may switch from shoreside operations to at-sea joint venture fishing, and they may move from bottom dragging to mid-water trawling. Beyond the confines of groundfish, trawl vessels may shift between pink shrimp and groundfish trawling. These are all important aspects of operational fexibility for vessel owners.

Three alternatives to the FMA/CDA proposal meriting consideration are (1) to include all gear types in the license limitation program, (2) to limit the scope to "major" groundfish species, and (3) to permit small catch levels by unlicensed vessels. Extension to all gear types would increase the size of the licensed fleet by an order of magnitude, but would bring the various fixed gear vessels under control early. This would address the potential future problem of expanding harvest capacity by an unregulated portion of the fishing fleet. Second, the idea of licensing only those vessels fishing "major" species would alleviate the need to include in the limited fleet every vessel that catches an occasional spiny dogfish or soupfin shark. Without restricting the program to major species, the extension to all gear types would undoubtedly make the system too all-inclusive and cumbersome.

A third option might be to allow unlicensed vessels to land groundfish so long as they remain below some low limit. All unlicensed vessels could be allowed, for example, to land up to 1,000 pounds of groundfish on any trip, or up to 10,000 pounds per year. This would permit the minor incidental catch of groundfish by trollers, shrimp vessels and purse seiners without adding these vessels (and the redundant harvest capacity they might represent) to a permanent licensed groundfish fleet.

MEANS OF LIMITING ACCESS

The FMA/CDA proposal is for a groundfish fishing license attached to the vessel. The principal alternative form of licensing, the personal fishing license, has been adopted in Alaska and elsewhere. The consequences of assignment to fishermen versus vessel owners are not immediately obvious. In Alaska it was thought that licensing fishermen would prevent cannery owners with corporate fishing fleets from financially dominating the local fishing labor force (Adasiak, 1978). The bargaining strength of vessel owners relative to licensed crewmen is weakened when the vessels owners cannot tap a large pool of new fishermen. Also in Alaska salmon fishing licenses cannot be used as collateral for loans and cannot be owned by corporations. These provisions were supposed to protect licensed fishermen from some possible threats to their continued participation in the fishery. Where vessel ownership is not divorced from fishing this issue is less important.

Choice between attachment to individuals or vessels must be made in designing IFQ's as well. If the 10,000 ton sablefish ABC were allocated as 500 20-ton IFQ's, these could be assigned on the basis of historical share to fishermen, to vessel owners, or even to corporations involved in fish processing. With personal IFQ's a trawl vessel owner would need to hire a skipper or crew member holding an IFQ. With shares assigned to vessels the owner would have control of the harvest right and fishermen not owning vessels would be at a disadvantage; and with corporate ownership of shares the processors could more easily plan and manage the fleet fishing for them.

A sub-option for IFQ's is the partial implementation of the system for a subset of groundfish stocks. One could allocate the estimated annual allowable catch of widow rockfish, sablefish or Dover sole while leaving other species out of the IFQ system. Also, as suggested by Robert Stokes in his study of north Pacific halibut, one could establish IFQ's for a portion of the total harvest of a given species while retaining a communal fishery for the remainder of the harvest. This option has the advantage of providing a choice to fishermen who, for whatever reason, do not want to join a quantitative rights system. If one-half of the traditional harvesters of Dover sole object to an IFQ system, one could distribute IFQ's for half the annual yield to those wishing to join the system. The traditional harvest sector would fish from January 1 until one-half of the annual ABC is taken. Fishermen with IFQ's could fish whenever they wish, and would probably schedule their harvest to maximize its landed value.

INITIAL ALLOCATION OF FISHING PRIVILEGES

The FMA/CDA proposal would allocate trawl licenses only to certain groundfish trawlers (1) landing at least 100.000 pounds, or (2) making at least 12 deliveries during 1984, or (3) demonstrating to an industry governing Board that they had prior involvement in the fishery and were active in the north Pacific or Bering Sea trawl fishery in 1984, or (4) demonstrating to the Board that they signed a contract or began construction or conversion of a trawl vessel during 1984. These qualifications would exclude very few groundfish trawl fishing vessels from the licensed fleet. For that reason, this initial allocation of harvest rights would create no significant reduction in harvesting capacity.

Whether licenses or IFQ's are considered, the basic choice here is between administrative assignment and some kind of "market allocation". Administrative assignments are universally chosen in existing limited access programs, largely because government agencies (and legislators) are reluctant to take away historically established fishing rights. As noted in the previous chapter, when government regulations are designed to correct technical problems of communal resource use. use rights are generally assigned to actual, historic users in order to avoid causing a redistribution of wealth. When developing new resources (offshore oil) or distributing public resources not previously used (National Forest timber), however, government mechanisms tend to use more market-oriented allocations (auctions and royalties) which extract resource value from the users.

A case could be made that both historic use and new uses are found in the Pacific groundfish fishery. Extensive historic use of most flatfish, rockfish and sablefish by commercial fishing fleets could establish an informal "ownership" of the right to harvest. At the same time, however, new or developing fisheries have no such specific historic use. Pacific whiting, shortbelly rockfish, sanddabs and possibly other groundfish stocks would be essentially "new" from this perspective. A mix of administrative and market allocation of initial harvest rights could be justified on this basis. Ultimately, there is no technically correct answer to the initial allocation question. Distribution of public resources can and has been done in many ways.

TRANSFERABILITY OF LICENSES AND QUOTAS

Under the FMA/CDA proposal the trawl licenses would be transferred with sale of the vessel, and could be shifted from one vessel to another by the owner if the licensed vessel is lost or if the owner wants to "up grade" or "down grade" his vessel. Although the license itself would not be salable under this system, it would be fairly easy to perform almost any kind of transfer. For example, if a licensed vessel owner wants to take his vessel to a different fishery, he could replace his vessel with another and then sell the new vessel with license. Or, he could sell the original vessel with license to another fisherman, who would then replace the vessel and sell the original vessel back to the original owner. There would be no apparent market value to a license, but the difference between vessel prices with and without a license would provide a good indication of license value. The restriction on salability simply makes transactions involving limited harvest rights a cumbersome and roundabout process.

An alternative to this is a fully salable license. If sufficient numbers of licenses or quantitative harvest rights (IFQ's) change hands on a routine basis, the market allocation of fishing rights would have all the advantages and disadvantages of market allocations that are experienced in other sectors of the economy. Market allocations are presumed to facilitate the efficient entry and exit of resource users. Less adept or profitable harvesters would be encouraged to sell their rights and enter a different line of work, while more efficient operators could expand. No coercion would be necessary, since anyone with a license or harvest right would have the option of not selling.

With vessel licenses as proposed by FMA/CDA sufficient transferability seems to be incorporated. For an IFQ system to work, however, true market sales would be almost a necessity. One alternative is for annual harvest quotas to be initially allocated among vessel owners in proportion to their historic shares. A vessel owner with a vessel that breaks down for an extended time would want to sell any quotas he owns to another operator. Also, a vessel which is harvesting mostly rockfish may want to shift into shrimp or Dover sole fishing. The owner will need to sell one set of quotas and buy a new set. Without the freedom of market sales, it would be difficult to maintain operating flexibility with quantitative harvest rights.

LONGEVITY OF HARVEST RIGHTS

In view of the long-lived investments inherent in both fishing vessels and fishing know-how, there seems to be no logical reason to have licenses or IFQ's expire annually or over a short period of years. The FMA/CDA proposal allows perpetual trawl licenses. Only if a vessel owner failed to meet minimum landing requirements and failed to seek an exemption for his vessel would a license be automatically retired. Personal licenses in Alaska and elsewhere are also perpetual. The Pearse Commission recommended that British Columbia salmon licenses be issued with a ten-year term, but that proposal was part of an intended fleet reduction program that would end with issuance of a smaller number of perpetual licenses.

In a limited access program incorporating all gear types, however, it might be useful to issue short-term licenses to vessels that really intend to fish only for a short time or which temporarily exceed some maximum harvest level allowed for unlicensed vessels. With a fully marketable IFQ system, anyone wanting to enter or leave the groundfish fishery temporarily would have the opportunity to do so.

MECHANISMS FOR ADJUSTING NUMBERS OF HARVEST RIGHTS

Under the FMA/CDA proposal the number of trawl licenses, once established, would change only where individual owners allowed their licenses to lapse. Because these licenses would be potentially valuable in the future, it would be unlikely that significant numbers of vessel owners would voluntarily withdraw from the licensed fleet. Assuming that there will be slow attrition from the trawl fishery, the FMA/CDA proposal calls for an annual review of the size and condition of the fleet. No specific procedures are included, however, for either causing more rapid decrease in the fleet or for increasing the number of licenses at some future time.

To achieve an economically efficient fleet size, some reduction in number of vessels would be necessary under a license limitation program. On the other hand, an expansion of the currently developable fisheries for Pacific whiting and shortbelly rockfish might justify adding to the fleet.

For fleet reduction, attrition and buyback programs are the only frequently discussed alternatives. For attrition to have much effect, there must be fairly stringent annual requirements for renewal of licenses, and the licenses must not be transferable to new fishermen. This approach, therefore, seems to impose a rather arbitrary distribution of fleet reduction burden among fishermen. Also, while waiting for attrition to take its toll, many fishermen may remain in the fishery after they should have left for health or safety reasons.

Buyback of vessel licenses provides a positive means of reducing the number of vessels, but it requires a source of funding. In their extensive review of buyback of fishing rights, Schelle and Muse (1984) found only one that was not a government subsidized program. If Congress and state legislatures are not prepared to provide financing, then fees and royalties from the fishery could be used to create a fund for buyback. A large number of technical issues need to be addressed in designing a buyback system, including (1) determining the target fleet size, (2) choosing whether to buy licenses only or to include vessels and gear, (3) whether to target the buyback on a specific distribution of vessel sizes and capacities, and (4) the specifics of the application and offer system.

An innovative means of reducing vessel numbers was implemented in the British Columbia roe herring license system (Macgillivray, 1986). The fishery was divided into three subareas and each licensed fishermen was allowed to choose one area. Licenses are salable, however, and a license owner may buy up licenses from all three areas. If management authorities stagger the openings of herring fishing seasons in the three areas, this method of fleet reduction allows consolidation of fishing operations with attendant reductions in fishing costs. Potentially, the total number of participants could fall to one-third the original number. In fact, from 1981 to 1985 the total number of licenses fell from 1557 to 1132. As of 1985 only 17 vessels had three licenses. It has been reported that the British Columbia system resulted in both improved product quality and reduced fishing costs.

Under an IFQ system, numbers of participants need not be adjusted directly. Instead, the quota initially allocated will be redistributed in private market transactions to determine the number of participants. With marketable IFQ's, adjustment of numbers of vessels or fishermen is not administered by the management program. Nevertheless, ownership of IFQ's may be restricted to some defined class of "qualified" fishermen, and the number of such fishermen may be of concern. It is difficult to anticipate what issues might arise under such a system in the absence of any experience with it or a specific proposal.

HANDLING DISPUTES

Disputes are likely to arise concerning the initial allocation of harvest rights (whether licenses or IFQ's), and in exercising the mechanisms for license transfer, renewal and termination. Most existing license limitation programs avoid disputes regarding initial allocation by including almost every conceivable claimant. Alaska's salmon license program did not, much to the chagrin of the Commercial Fisheries Entry Commission. The Alaska system required the Entry Commission to establish means of determining the extent to which applicants met various criteria concerning historic participation, and dependence on the fishery. Challenges of the Commission's procedures and decisions still, after ten years of operation, constitutes a significant portion of the Commission's business. This could be avoided by establishing quantitative criteria in law or regulation at the outset, rather than leaving interpretation of some vague criteria to a quasi-regulatory body.

To deal with the disputes that occur, several alternative procedures could be established. A review board dominated by fishermen and other industry members could decide whether individuals should be given licenses and whether proposed license of vessel tranfers should be allowed. A variant on this is to use the board to make recommendations to an agency administrator (e.g. an NMFS Regional Director) who would make an official ruling. Fishermen affected by decisions of the Board may feel that they will get a more sympathetic hearing before their peers than before a non-fishing administrative or judicial panel. On the other hand, both fishermen and the public at large may occasionally fear that conflicts of interest or favoritism are more likely to affect the decisions of an industry-dominated review board.

Other approaches could include use of an Administrative Law Judge (ALJ) to hear evidence and make recommendations or rulings. Agency administrative procedures could be used to hear grievances and make rulings. In any case, a fisherman has access to the courts to seek redress of arbitrary or wrongful actions by the management agency.

CONCLUSIONS

The basic elements of a limited access program can be developed and combined in almost infinite variety to meet the specific needs of a particular fishery and its circumstances. This chapter has introduced and explained many of the most commonly-discussed alternatives. These were grouped into seven categories ranging from scope of the fishery to means of dispute settlement. The trawl license moratorium proposal submitted by the Fishermen's marketing Association and Coast Dragger's Association provided a useful benchmark for comparison which helped to clarify the explanation of other options. Further innovation in developing variants on these alternatives will be important for fishermen, managers and scientists involved in using limited access programs for public fisheries management.

TABLE 1. LIMITED ACCESS PROGRAM ELEMENTS AND OPTIONS

I. Scope of Fishing Activities to be Restricted or Allocated

A. Types of Fishing to be included -	1. All commercial and recreational
	2. All commercial plus for-profit party and charter boat fishing
	3. All commercial fishing
	4. Just "big-time" commercial operations, such as those landing at least 50 tons of groundfish per year.
B. Geographical extent -	1. All Pacific coast including at-sea sales
	2. All Pacific coast shoreside landings
	3. Pacific coast shoreside harvests from the 3-200 nautical mile zone (FCZ, excluding State waters) .
	4. Harvests in certain selected INPFC areas such as the Vancouver or Columbia areas.
C. Fishing Gear Types	1. All gear including groundfish trawl, hook and line, fish pots, gill nets and shrimp trawls.
	2. Control only "directed" fishing with trawl gear, fish pots and gill nets.
	3. Control only the major gear type - trawls (see FMA Proposal).
D. Species of Fish	1. All species listed in Groundfish Fishery Management Plan
	2. Include only "important" groundfish species (e.g. all rockfishes, whiting, sablefish, Dover sole, English sole, petrale sole, Pacific cod, ling cod).
	3. Focus harvest permits or rights on single species or logical groups of species. For example, a "rockfish" permit or a "whiting" joint venture permit.

Figure 1 continued.

II. Means of Limiting Access to the Fishery

- A. License Limitation
  1. Personal License to fish (with or without limiting to "natural persons").
  2. License attached to vessel
  3. License attached to gear (e.g. net)
  4. Dual system: fishing license for people plus vessel or gear permits.
- B. Individual Fisherman Quota (IFQ)
  1. IFQ conveys right to take a share of the allowable yield of specific stocks.
  2. IFQ conveys right to take annually a specified quantity from a specific stock.
  3. Annual yield is assigned to a company or fisherman's cooperative to be sub-divided among fishermen. ("Enterprise quotas")
- C. Taxes, Royalties and Fees
  1. Set initial entry fees high enough to discourage excessive participation.
  2. Establish landings royalties for fully utilized species.
  3. Establish annual license renewal fees.

III. Basis for Initial Allocation of Harvest Rights

- A. Administrative Assignments
  1. Include all persons or firms with recent record of landings. (e.g. landed at least one fish in the past five years)
  2. Include all applicants within a specified time period.
  3. Include all persons or firms meeting minimum landings requirements.
  4. Hold a lottery among all applicants.
  5. Include all persons meeting certain qualifications as commercial fishermen.
- B. Competitive Market Allocation
  1. Auction off limited number of fishing licenses or IFQ's.
  2. Sell licenses or IFQ's at prices calculated to reflect market values.

Figure 1 continued

IV. Transferability

- A. Non-transferable
    1. Retirement or death causes termination of fishing license or harvest right; may revert to State to be re-issued.
    2. Ownership transfer no allowed, but owner may lease or lend fishing right.
- B. License or IFQ attached to specific vessel or gear.
    1. Transfer requires sale of vessel or gear.
    2. May be transferred among vessels of equal fishing capacity.
    3. May be subject to clearance by State and qualification of new owner.
- C. Fully transferable at discretion of owner.
    1. Market sales may be subject to clearance by State fisheries agency or review board
    2. State may require that new vessel have no more harvest capacity that previously licensed vessel.

V. Duration of Term of Fishing Right

1. Perpetual. The license or IFQ can be used as long as the owner wishes.
2. Annual, renewable or non-renewable. Renewal could be automatic or could depend upon continued participation in fishery.
3. Dependent upon lifetime or career of permit holder. License or right expires upon death or retirement of holder.
4. Fixed, multi-year term. License or IFQ might confer right to fish for, say, ten years.

Figure 1 continued

VI. Means of Altering Number of Licenses or Fishing Rights

A. Fleet Reduction	1. Attrition through retirement, termination, revocation for cause.
	2. Buy-back of perpetual or long-lived licenses by State or Federal agency.
	3. Automatic expiration of fixed-term licenses in conjunction with issue or sale of reduced number of new licenses.
B. Increase in number licenses or rights.	1. Lottery among "qualified applicants".
	2. Sale to applicants at agency-established price.
	3. Selection of new licensees on first-come, first-served basis.
	4. Auction of new licenses or rights in competitive market open to all.

VII. Settling Disputes Regarding Issuance and Transfer of Fishing Rights

A. State/Federal Court	The fishermen can ultimately seek redress in the courts under any of the options.
B. Administrative Law Judge (ALJ)	1. ALJ could make a final administrative ruling after hearing with fisherman
	2. ALJ could make recommendation to agency administrator after hearing issue.
C. Special Appeals or Review Board	1. A board of peers (industry representatives) could make rulings or recommendations to agency administrator.
	2. A board of disinterested citizens could hear disputes.
D. Agency Administrator	1. Administrator could make final rulings for agency (e.g. NMFS Regional Director).
	2. Administrator could be bound to pass issue to Federal department head.

Elements of a Proposal for a Groundfish Trawl License Moratorium by the Fishermen's Marketing Association and Coast Draggers Association

1. A trawl license would be established by legislation in the states of California, Oregon and Washington which would create a groundfish trawl license and simultaneously place a moratorium upon their issuance. The legislation would become effective only when all three states have adopted similar legislation.

2. A regional groundfish trawl license would be established with the license assigned to a particular vessel. This license would allow the vessel to operate in the waters adjacent to and deliver groundfish to the states of Washington, Oregon, and California. The license may be transferred with sale of the vessel.

3. An industry governing Board should be established. This should be a tri-state Board composed of one person representing the directors of the three state fisheries departments and nine active trawl vessel owners. The director's representative should act as chairman of the Board and vote only in case of a tie. The person selected to represent th directors should rotate annually amongst the three states. There should be three vessel owners selected by the Governor or Director of each state. The selection should be made from a list of names submitted by a trawl association or individuals at large. The vessel owners should serve three year terms staggered on one year intervals.

A quorum for the Board should be five vessel owners with at least one vessel owner form each state present. Actions requiring the approval of a vote should pass with a simple majority of members present.

4. Funding of the administration and cost of the Board meetings should be covered by the levy of a flat fee of $100 per vessel. This fee should be collected when the vessel owner purchases his commercial license.

5. In order to receive a license a vessel must meet an initial qualification of either delivering 100,000 pounds of groundfish or making at least 12 deliveries of groundfish during 1984 using legal trawl gear for groundfish as defined by the Pacific Coast Groundfish Management Plan. This qualification cannot be met by delivering incidentally caught groudnfish from another fishery.

6. In order to maintain a license a vessel must continue to meet the initial qualifications of 100,000 pounds or 12 deliveries on an annual basis. If a vessel owner knows beforehand that his boat will not be able to meet the continuing qualifications because of removal of the vessel from the groundfish fishery into another fishery, he may request an exemption form the governing Board in advance.

7. Individuals with a contract signed during 1984 or have begun new construction or conversion during 1984 shall qualify for a license. However, the governing Board must first verify the validity of such contracts for or initiation of construction or conversion.

8. The governing Board may grant licenses to anyone based upon prior involvement in the fishery, provided they have remained active in the trawl fishery in the Northeast Pacific or Bering Sea and they appeal for the license during the first year of this moratorium.

9. Unconditional replacement of vessels should be allowed. Replacement of vessels lost due to sinking or the desire to upgrade or down-grade should be allowed. If a person wishes to up-grade or down-grade with a second vessel the original vessel must be removed from the fishery.

10. The size and condition of the fleet should be reviewed annually. The size of the fleet will slowly decrease through attrition. An annual review should establish if the fleet is higher than, equal to, or below the optimum level in relationship to stock size and market demand.

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A Review of California`s Limited Entry Programs

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INTRODUCTION

Access to California's commercial fisheries has been increasingly restricted through a variety of limited access programs. Until 1974, when the state limited the number of licenses in the herring roe fishery, all of California's fisheries operated under the traditional open access system. Commercial fishing vessel registrations and annual commercial fishing licenses have long been required by the state, but these were available to all applicants at a nominal fee. Since 1974 seven restrictive licensing systems have been established, and the pace of change in the licensing systems seems to be accelerating.

The California Department of Fish and Game (CDF&G) distinguishes three different types of limited access systems: (1) qualified entry, (2) entry moratorium, and (3) limited entry. The first type is designed to assure that fishermen are knowledgeable and/or experienced in a fishery before they are permitted to operate a vessel in that fishery. For example, the Fish and Game Commission requires that new recipients of gillnet permits meet specific qualifications. These include having either a year's experience as a crew member on a licensed vessel, a history of activity in the fishery, or a passing score on a proficiency examination administered by CDF&G. Qualified entry programs do not place a limit on number of participants in a fishery, but they may slow down the pace of new entry.

A moratorium on new permits puts a stop to all new entry and is usually a preliminary step to setting up a limited entry system. As the name implies, a moratorium freezes the number of permits issued for a particular fishery as of a specific date. Although a moratorium temporarily permits no new entry, it also seeks no reduction in numbers of fishermen. Two examples are the 1980 temporary moratorium on salmon fishing licenses (replaced with a limited entry system in 1982) and the moratorium on general gillnet fishing permits that went into effect on January 1, 1986. Implementing legislation for the latter moratorium requires CDF&G to prepare a report assessing the need for a limited entry program for the gillnet/trammel net fishery by January 1, 1989.

A full-blown limited entry program has specific procedures and conditions for licensing new fishermen. California fisheries under limited entry programs include (1) the herring roe fishery, (2) the commercial abalone fishery, (3) the salmon fishery, (4) the drift gillnet fishery for shark and swordfish, (5) the experimental driftgill net fishery for swordfish off central California, and (6) the nearshore set gillnet and trammel net fishery off central California. Some of these programs set goals for total numbers of participating fishermen or vessels. Others simply control the conditions of entry. The legislature did not establish numerical goals for the salmon limited entry system, for example, but it did require that the Commercial Salmon Fishing Review Board and Fish and Game Commission determine the number of new permits to be issued annually. In contrast, the Fish and Game Commission set a specific goal of 100 operators in the abalone license limitation program.

This paper describes the objectives sought and principles adopted in California's limited access systems, followed by a brief description of each existing program. The final section offers a summary and some observations regarding present difficulties and future directions for limited access systems in California.

PRINCIPLES AND OBJECTIVES IN CALIFORNIA'S PROGRAMS

California's limited access programs have sought a wide variety of objectives, including (a) to enhance conservation of fish resources, (b) to protect the commercial fishing industry, (c) to reduce the numbers of incidentally killed marine mammals and seabirds, (d) to minimize potential conflicts between competing commercial fisheries and between sport and commercial fisheries, and (e) to "insure efficient and economic operation of the fishery." Only the experimental central California drift gillnet swordfish permit program fails to mention fish stock conservation as an objective. That program seeks "to allow increased access to the swordfish resource." The central California gill and trammel net program is most concerned with incidental take of mammals and birds, while the drift gillnet shark and swordfish program seeks to minimize conflicts and to conserve shark populations. Only the herring roe license limitation program includes economic efficiency as a specific objective.

Our review of stated objectives for limited access programs reveals that traditional notions of physical conservation and equitable allocation remain central to the state's conception of its role in regulating commercial marine fisheries. Stability of the fishery and reduction of social conflicts play somewhat smaller roles. The standard economic objectives of efficiency and rent-maximizing have a minimal influence on California's decisions. CDF&G personnel have frequently stated that CDF&G is primarily responsible for conservation of the fish stocks and secondarily for the resolution of user conflicts, while the industry itself must take the lead in developing management programs specifically intended to increase economic efficiency.

Besides avoiding economic efficiency objectives CDF&G generally prefers to prevent fishery permits from becoming assets of value to individual fishermen. When transferable permits are sold on the open market, they may take on significant value, as has happened in Washington and Alaska. Two objections are raised to the transferable permit. One objection is that potential regulatory problems may arise when fishermen with a substantial investment in their permits resist necessary restrictions on the fishery. A second and more important objection is that a substantial price attached to a transferable permit represents a windfall gain attributable to the newly created property right. Furthermore, this permit price creates a discriminatory barrier to new entrants. Only those citizens who inherit a permit or are sufficiently affluent to purchase one will have access to the fishery. These objections have extensively influenced the character of all limited entry programs in California.

Transfer of permits to heirs and working partners is permitted under specific conditions in all California limited entry programs. For example, a spouse, child or sibling of a deceased, retired or incapacitated permittee can obtain the permit if proof can be given of physical, working participation, aboard the permittee's vessel, in the limited entry fishery.

There are some additional common characteristics found in California's limited entry programs. Eligibility for initial permits is based upon past participation in the fishery or upon substantial investment prior to the enactment of the limited entry or moratorium program. California law specifically permits entry during the first year of a limited entry program to any commercial fisherman with twenty years of general experience and at least one year of participation in the target fishery. Permits are generally issued annually, and retention of permits from year to year is often contingent on continued participation in the fishery. Permits may not be held by corporations or partnerships and are attached to the person except in the salmon fishery, where they are attached to vessels. Allocation of new permits when they are available is generally based upon qualifications, including past participation and experience. Selection among equally qualified applicants is usually accomplished through a drawing.

LIMITED ACCESS PROGRAMS

Herring

The modern California herring roe fishery began in the San Francisco and Tomales Bays to satisfy Japanese demand during a period of shortage and high roe prices in the early 1970s. Salmon sport fishermen and local residents were disturbed and concerned by the sudden emergence of the fishery. At their behest, legislation was introduced in 1974 to prohibit commercial take of herring except for use as bait. Before the beginning of the 1974 winter fishing season, CDF&G negotiated a compromise bill which gave the agency authority to establish a permit system and an annual catch quota. During 1974 and 1975 the number of permittees was limited to the number of participants in 1974--seventeen. Participants were chosen by drawing from among qualified applicants. As roe prices escalated, CDF&G was pressured to allow additional fishermen to participate. In 1976 a total of 57 fishing vessels were licensed to fish in the two bays.

The limited entry system established in 1977 allowed a total of 267 vessels to enter. All previous participants were "grandfathered" into the fishery and an additional 150 new licenses were allocated in 1977. That number steadily increased to 447 in 1982. To qualify for renewal, a permittee must have had a valid permit the previous year and must have actively fished, or demonstrated an intent to fish, the previous year. Permits cost $50 per year and may be revoked for fishing violations.

In addition to control over the number of participants, the management system enforced quotas based on spawning biomass estimates derived from surveys of roe depositions in the bays. To reduce the congestion and competition in restricted fishing areas, an odd-even platoon system for gillnet vessels was introduced. Vessels with odd-numbered permits fished during odd-numbered weeks, and vessels with even-numbered permits fished during even-numbered weeks. In addition, a small number of purse seine and lampara vessels were licensed to fish. A third "experimental" gillnet platoon was added in 1980, and these vessels are permitted to fish only during the month of December, before the opening of the traditional fishery in January.

The increasing complexity of regulations was not necessitated by fish stock depletion. In fact, spawning biomass estimates indicated that herring populations were increasing. Management measures were designed more to alleviate social problems than to provide protection to the resource. Intense fishing pressure was motivated by extremely high ex-vessel prices. The reported price rose to nearly $4,000 per ton in 1980. A highlining purse seine vessel in 1979 reportedly sold more than $120,000 of fish in little more than two weeks. The prospect of extraordinary profits brought intensely competitive fishing into a part of San Francisco Bay that is highly urbanized and environmentally sensitive. Fishing boats were competing for limited space with each other, commuter ferries, and yachts. If the resulting conflicts had not been addressed, non-fishing interests would have pushed harder for prohibition of the commercial fishery.

A nine-member advisory committee was formed to advise the CDF&G director on annual regulation changes. The Fish and Game Commission establishes a maximum limit of permits to be issued by gear type and area. These permits are issued to the owner, operator or leasee of a fishing vessel. The vessel to be used must be specified in advance, and the permits are nontransferable, except that permittees may designate another fishing vessel under certain circumstances.

New permits are issued whenever the number of permits allowed exceeds the number of renewals. Applicants must be licensed commercial fishermen and must own, operate or lease a currently licensed fishing vessel. The method of selection is a public drawing from among the qualified applicants.

Abalone

The abalone limited entry system adopted in 1977 was one aspect of a comprehensive program established by the Fish and Game Commission with the goal of restoring abalone stocks and increasing yields. After an intensive study it was concluded that one cause of declining abalone stocks was mortality of abalone under legal size that were picked and replaced. This problem was largely due to the excessive number of divers in the fishery, many of whom were inexperienced. From 1973 to 1975, 30 percent of the divers active in any year were new to the fishery and about 50 percent had less than 2 years' experience. CDF&G, with the support of industry organizations, recommended a limited entry program to remove inexperienced divers from the fishery and to reduce overall fishing effort to reasonable levels. The Fish and Game Commission established a limited number of nontransferable diving permits and made provision for issuing new licenses when the number of permittees fell below a set number. Crew members are also required to purchase permits, but there is no limit on the number of crew permits. Diver permit fees were set at $200 annually and crew permits at $100.

In 1977 licenses were initially issued to 397 divers who had participated in 1976. Annual renewal of the license requires a minimum landing of 6,000 lbs or 20 landings, defined as a minimum of two dozen abalone per landing. Permittees may obtain a waiver of the minimum landing requirement under certain circumstances. Permits may be revoked due either to failure to meet minimum landing requires or to fishing violations. From 1976 to 1985 the number of diver permits issued dropped from 397 to just under 1975. In

1985, further amendments to the regulations established the target number of diving permits at 100. To qualify, new applicants for permits must have at least three years experience as an abalone diver or crew member or must pass a proficiency test. When there are more applicants that permits available, a public drawing is held among qualified applicants.

Salmon

During 1979 the California legislature passed a bill establishing a two-year moratorium on participation in the commercial salmon fishery. This followed a recommendation from the Pacific Fishery Management Council calling for all Pacific Coast states to limit entry into the salmon fishery. The stated objective was to halt the increase in fishing effort while the merits of a permanent limited entry program were examined. Some concern regarding the salmon fleet was warranted by the long-term trends in the fishery. Between 1960 and 1978, the number of commercial vessels landing salmon in California grew from 1,365 to 4,919, while inflation-corrected ex-vessel value of salmon landings per vessel fell from $8,290 to $3,460 (in 1985 dollars).

The moratorium required commercial salmon vessel operators to have a salmon validation permit as well as the usual California commercial fishing license and a salmon stamp. This validation permit was nontransferable and revokable. Each permit holder was authorized to have up to two crew members on board with him who were not qualified individuals, and, after approval of a substitution application submitted to CDF&G, he could have another person serve in his place under his permit for up to 15 calendar days.

To qualify for a salmon validation permit, an applicant needed to show only that he or she had sold at least one salmon during at least one of the years 1974 through 1979, or that he had possessed a commercial fishing license and assisted with the capture and sale of at least one salmon, or that he had made a substantial investment in becoming a commercial salmon fisherman in California during the qualification period. During 1980, a total of 5,119 troll vessels landed salmon in California. In 1981 the number dropped to 4,102, and in 1982 the number of active trollers in California was 4,013.

During the moratorium various segments of the commercial industry in California, led by the Pacific Coast Federation of Fishermen's Associations, developed a comprehensive proposal for a limited entry system. As amended and enacted into law, the limited entry system creates a commercial salmon vessel permit which is issued to owners of vessels used to land salmon in California during 1980-82, to persons who possessed a commercial salmon permit under the moratorium and who had under construction or contracted for construction a vessel for entry into California's salmon fishery, and to other persons who meet specific criteria as determined by the newly-created Commercial Salmon Fishing Review

Board. The permits are to be renewed annually by application to CDF&G. They may be suspended or revoked by the Fish and Game Commission for violation of fishing regulations or because application for renewal is not submitted.

A person may gain new entry to the fishery by purchasing a vessel already licensed under a vessel permit. Licenses are attached to vessels and cannot be sold or transferred separately from the vessels. If a licensed vessel is lost or retired from the fishery, the permit is reissued to the vessel owner and can be placed on another vessel within one year if that new vessel has a salmon fishing potential no greater than the original vessel, as determined by the review board. New entry may also be obtained by application for a new vessel permit issued by CDF&G. New permits may be issued by lottery in the future, under criteria to be established by the review board. The number of new permits is to be based upon the health and status of the salmon resource, and on the economic stability of the commercial salmon industry. To date, no new vessel permits have been issued.

The salmon limited entry system is still an interim system. To devise a permanent system the law calls for collection of information on the salmon fishery, including the impact that equipment and experience have on the fishery; and submission to the legislature of a report containing this information. Originally the interim system was to expire on January 1, 1986, but it has been extended. During the first three years of operation of the new system, the number of vessels landing salmon in California has dropped from 3,223 in 1983 to 2,308 in 1985. The number of permits issued dropped from 4,617 to 3,712 during the same three-year period. The shrinking fleet size is largely due to diminishing abundance of salmon stocks, which necessitated increasingly restrictive ocean fishing regulations, and to a host of adverse economic conditions. No buy-back or other directed fleet reduction program has been enacted.

General Gillnet Permits

These general permits were created in 1981 to apply to all state waters. This permit program constituted a "qualified entry system" until a moratorium on new permits was established on January 1, 1986. These are annually renewable, nontransferable, revokable permits issued to applicants who have worked for at least 12 months on vessels using gillnets or trammel nets, or who have passed a proficiency examination administered by CDF&G, or who have landed at least 10,000 lbs of fish worth at least $10,000 during a 12-month period, or who have landed at least 1,000 lbs of fish taken in gillnets in at least four of the five license years prior to date of application. Until 1986 there was no specific attempt to limit the numbers of such permits. The qualification requirements and annual $50 fee may have restrained entry somewhat.

The new moratorium prevents the issuance of new gillnet or trammel net permits except to people applying before January

1, 1986 to take the examination, and then passing it. Renewal of existing, valid permits is allowed; and permit holders having landed fish in at least 15 of the preceding 20 years may transfer their permits to other qualified persons. CDF&G is to prepare and submit to the legislature by January 1, 1989 a report assessing the need for recommending a limited entry program for gillnet permits. The temporary moratorium expires on January 1, 1990.

The permit moratorium was accompanied by additional restrictions on the use of gill and trammel nets in harvesting California halibut. These included altered minimum fish size limits, a requirement that mesh size be no less than 8 1/2 inches, and a limit on the amount of net to be fished by any permittee to 1,000 fathoms (6,000 ft). All those fishing under the drift gillnet and gill/trammel net permit described below must also possess one of these general gillnet/trammel net permits.

Drift Gill Fishery for Shark and Swordfish

In the late 1970s it was found that drift gillnets with greater than 8 inch mesh size are effective at capturing thresher shark, bonito (or mako) shark, and swordfish. A new fishery developed, primarily in southern California waters, using this gear, but it faced several problems that resulted in public pressure to limit or eliminate the fishery. First, the use of drift gillnets to take swordfish provoked a "turf battle" for swordfish with the established harpoon fishery. Secondly, the reported take of marlin, a species strictly reserved for recreational fishing in California, was a severe provocation to numerous and influential recreational fishing interests. Thirdly, scientific research suggests that the shark populations are relatively slow-growing due to low reproductive rates, and that they could be rapidly depleted by excessive fishing. Finally, protected marine mammals (such as the California gray whale) can be inadvertently entangled, harmed and killed by the nets. All of these factors contributed to political pressures which called for limiting entry.

Initially, most of the fishing covered by this permit occurred south of Point Arguello, but it was not limited to the southern California region. Drift gillnet fishing spread as far north as Oregon and out to sea beyond 200 miles. A special permit for shark drift gillnet fishing was instituted in 1980. These nontransferable, revokable permits were initially issued to persons who had taken shark by drift gillnet in 1978 or 1979, or who had made prior significant investments in the fishery. The program also established a permit fee of $150, restrictions on the size of nets used, restricted fishing seasons, a logbook requirement, and an observer program. The 1980 regulations also included allowable incidental catch tolerances for marlin and swordfish. Permit holders are required to designate which vessels they intend to use, but they may transfer to another vessel after notifying CDF&G by written request.

In 1982 the program was modified to reduce fishing effort on the highly depletable shark populations by implementing a limited entry system with a target limit of 150 permits. Because more than 200 permit holders were active in 1982, no new permits were to be issued until the number of active permits fell below the target fleet size. In addition, modifications were made to unrestrict the catch of swordfish, to close the fishery from February 1 through April 20, to reduce the incidental take of marine mammals, and to establish various other time-area closures which reduce conflicts with commercial harpoon and recreational marlin fishermen. In order to provide additional protection to thresher sharks, in 1985 additional regulations were implemented that prohibit fishing within 75 miles of the coast during June 1 to August 15. In effect the program now recognizes the drift gillnet as a directed swordfish fishery, which needs to be managed to protect the marine mammals and thresher shark populations and to reduce conflicts between the drift gillnet fishery and other sport and commercial fisheries.

Central California Special Gillnet and Trammel Net Permits

The gillnet and trammel net fishery for halibut, white croaker and rockfish in central California between Monterey and Point Reyes (including the Gulf of the Farallons) expanded rapidly in the early 1980s. The number of general gillnet permits issued in central California increased from 97 during 1981 to over 500 during 1984. Many of the new fishermen were recent immigrants from southeast Asia. As with the southern California drift gillnet fishery, the growth of the gillnet and trammel net fishery spawned tensions and controversies with better-established commercial fishermen, recreational fishermen, and other marine interests. Of particular concern was the widespread killing of seabirds and marine mammals in the nets deployed in nearshore, shallow water. Many of the birds and mammals affected are legally protected by the Migratory Bird Treaty Act, the Marine Mammal Protection Act and the establishment of the Point Reyes/Farallon Island National Marine Sanctuary.

All commercial operators in this fishery were, of course, required to obtain general gillnet and trammel net permits. Under intense public pressure to resolve the incidental mortality problem, the state restricted the use of the nets in shallow waters (waters of less than 10 fathoms in depth). After extensive meetings between CDF&G personnel and concerned groups, the legislature passed a bill in 1984 expanding the closed areas, creating closed seasons, restricting the allowable length of nets, and requiring that fishermen obtain a nontransferable special permit to use a set gill or trammel net in the nearshore area (generally within 3 miles of land) off San Francisco and other central California areas. Licensed gillnet fishermen operating further offshore are not required to have this special permit. Some closed areas and seasons were designed to protect sea otters in Monterey Bay and to protect sea lions and harbor seal rookeries at Ano Nuevo Island. Others were intended to reduce seabird mortality and to reduce conflicts between gillnet fishermen and salmon troll fishermen in the Farallon Islands.

Fishermen were issued new special gillnet permits until March 31, 1986. To obtain a permit, a licensed owner or operator of a vessel must have possessed a valid general gillnet permit and must have presented evidence of (1) 10 or more landings of halibut, croaker or rockfish caught by net, or (2) an investment of at least $2,000 in nets, or a net reel, or other kinds of gear; this investment had to be substantiated by receipts and matching cancelled checks. (This requirement was a problem for the southeast Asian refugee fishermen, most of whom do business in cash; the problem was remedied through subsequent legislation.)

Since April 1, 1986, only previous permittees who have demonstrated involvement in the fishery have been able to renew. Each permittee may miss one year out of five in order to fish in some other fishery.

The number of permits for the fishery is now limited to 135. When the number of annual renewals falls below 135, new permits will be allocated by a random drawing among qualified applicants. An annual renewal fee of $125 is levied on permit holders. The permit system is scheduled to expire on April 1, 1989. CDF&G is required to prepare a report before the expiration date determining the optimum number of gillnet fishermen for the fishery.

Central California Experimental Drift Gillnet Swordfish Fishery

To allow increased access to the biologically healthy swordfish population off California, 35 experimental fishing permits were created in 1984. These nontransferable, revokable and annually renewable permits were made available to persons holding a valid general gill and trammel net permit, possessing a California commercial fishing license in each of at 10 previous years, and having a gillnet with mesh of at least 14 inches and a net reel for retrieving the net. If there are more than 35 qualified applicants, the 35 permits are allocated by random drawing. All permit holders can renew without demonstrating participation. If not all 35 permittees apply for renewal, the excess permits will again be distributed by random drawing to new applicants who meet qualifying conditions. Since holders of drift gillnet permits in southern California may also fish north of Point Arguello, this special license does not limit the number fishing in central California, but it does prevent the central California special permittees from fishing in the south.

A fee of $150 is charged for the permit. Restrictions on the use of this experimental permit are similar to restrictions on drift gillnet fishing south of Point Arguello. These include a maximum length of net (no longer than 6,000 ft), prohibition of fishing within 12 miles of shore, closure of the Gulf of the Farallons, a closed season from February 1 from August 15, and a requirement that nets not be in the water from two hours after sunrise to two hours before sunset.

CONCLUSIONS

Our review of limited entry programs in California provides ample evidence that this form of fishery regulation can be adapted to a wide range of circumstances and can be implemented in combination with various other regulations. The systems have been tailored to each fishery's particular problems, needs, and political situation. Although California has not ventured beyond the nontransferable fishing license, it has explored a surprising number of variations of license limitations. Licenses are limited by gear (general gillnet) or species/gear combination (salmon troll, abalone diver), or gear and area (drift gillnet). In the case of San Francisco Bay herring roe fishermen, an almost inconceivably complex set of regulations has been developed (two gears, two platoons of gillnets, special "experimental" permits, annual quotas split into gear types, individual seasonal catch limits for purse seine vessels, etc.).

Initial allocation of permits generally "grandfathers in" all past participants (at least if they have written documentation), and all limited entry systems provide means for new fishermen to enter when there are additional permits available. Although the criteria are not clear for determining the optimal number of permits in some fisheries (and are still being studied for salmon troll and gillnets), the bureaucratic mechanism for regulating entry at the desired level has been established. Discussions are currently proceeding on future limited access systems for sea urchin divers, groundfish trawlers and lobster fishermen.

The licensing programs have established useful overall limits on new entry to many of the state's crowded commercial fisheries. In several instances the limited entry systems are simply one part of a complex regulatory response to serious social and political pressures. Some of the fisheries (herring roe and possibly inshore gill/trammel net) could have been legislated out of existence if the license limitation response had not been invoked. Thus the permit system can be rated a success at dealing with some social and political difficulties. Also, where limiting entry has placed an upper bound on fishing effort, it has probably enhanced the efforts to reduce mortality of seabirds and mammals and may provide some protection to easily overfished shark populations.

Conservation policies behind California's limited entry systems have not begun to deal explicitly with the standard economic issues concerning commercial exploitation of depletable resources. The state government has not publicly acknowledged the need to assess economic aspects of fisheries, including the assessment of potential economic rent, effects of regulations on "capital stuffing" and overcapitalization in the fishing fleet, and equitable allocation of net resource values and resource management costs. Some of the limited entry legislation calls for a report on optimal or desirable number of licenses. This may imply a need for detailed economic analysis, but it is not yet clear how CDF&G and the Fish and Game Commission intend to deal with the economic issues. Past policy has tended to ignore these by insisting that CDF&G has no such responsibility and that the industry should develop proposals to deal with economic factors.

The history of commercial fisheries regulation clearly suggests that this is an unrealistic approach; private industry does not normally deal very successfully with overall economic efficiency issues in the absence of clearly defined property rights in the fish populations. So long as California's governing institutions adhere to the concept of "public resource" in ocean fisheries, and prefer to allocate fishing rights through public administrative rather than private market systems, it is likely that California will continue to use nontransferable fishing license systems.

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THE INFLUENCE OF BLOOD GAS PROPERTIES ON GAS TENSIONS AND pH OF VENTRAL AND DORSAL AORTIC BLOOD IN FREE-SWIMMING TUNA, *EUTHYNNUS AFFINIS*

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SUMMARY

We have developed a technique for capture, anaesthetization, instrumentation and release of tuna and have made the first determinations of blood gas values in dorsal and ventral aortae of free-swimming tuna. Dorsal aortic P_{O_2} varied from 34·5 to 91·7 mmHg, and P_{CO_2} ranged from 3·7 to 7 mmHg. Dorsal aortic blood [pHa = 7·77 ± 0·04 (8), mean ± one S.E.M. (*N*)] was more alkaline than ventral aortic blood [pHv = 7·65 ± 0·02 (7)]. Warming dorsal aortic blood from 25 to 35 °C in a closed system caused P_{O_2} and P_{CO_2} to rise and pH to fall. Oxygen-combining curves for whole blood were sigmoid [mean Hill's number = 1·72 ± 0·05 (11), range 1·57–2·0] and P_{50} over the pH range found in free-swimming animals was 21 ± 1·75 (8) mmHg. The CO_2-induced Bohr coefficient ($\Delta \log P_{50}/\Delta$ pH) was −0·59 ± 0·046 (30). Unusual features of CO_2-combining curves are attributed to a significant Root effect. Although these *in vitro* properties of tuna whole blood are at variance with other published data on tuna they nevertheless substantiate our determinations made *in vivo*.

INTRODUCTION

In a recent paper, Cech, Laurs & Graham (1984) reported some unusual features of the oxygen-combining properties of whole blood of freshly caught albacore tuna (*Thunnus alalunga*). They found that the oxygen dissociation curve was hyperbolic (Hill's number = 1·1) with an extremely low P_{50} (about 8 mmHg) even at 25 °C. There was a strong Bohr effect (Bohr coefficient = −1·17), a negligible Root effect, and a reverse temperature effect with $\Delta H = +1{\cdot}72\,\mathrm{kcal\,mol^{-1}}$ (at 0 % CO_2) and $\Delta H = +0{\cdot}26\,\mathrm{kcal\,mol^{-1}}$ (at 1 % CO_2). Unusual temperature effects on tuna haemoglobin solutions and whole blood have been reported previously (Rossi-Fanelli & Antonini, 1960; Sharp, 1975; Carey & Gibson, 1977, 1983; Ikeda-Saito, Yonetani & Gibson, 1983) and have provided a basis for models describing how oxygen transfer from the arterial to venous circulation would be minimized when blood is warmed in

Key words: oxygen dissociation, Bohr coefficient, Root effect.

the vascular heat exchanger before going to the muscles (Carey & Gibson, 1983; Cech *et al.* 1984).

Using these observations on whole blood, together with parameters chosen to illustrate performance of models, we can predict what the consequences would be for tuna going about their daily business. High ventilation volumes (Stevens, 1972) and large gill areas of tuna (Muir, 1969; Muir & Hughes, 1969) support claims that arterial P_{O_2} will be high and P_{CO_2} low. In fact, low P_{CO_2} is a prerequisite for effective performance of the models because the reverse temperature effect is greatly reduced by increasing CO_2 in the blood (Cech *et al.* 1984). The low P_{50} obtained by Cech *et al.* (1984) suggests that ventral aortic P_{O_2} will be low (<8 mmHg) if the animal is going to extract enough oxygen from arterial blood. Finally, the linkage equation states that the Bohr coefficient is identical to the Haldane coefficient (Wyman, 1964; Heck, 1970); if this holds for whole blood, as well as haemoglobin solutions, then if the Bohr coefficient exceeds $-1{\cdot}0$ dorsal aortic blood will be less alkaline than ventral aortic blood unless the RQ is also greater than 1·0.

Obviously, it is possible to test all the above assumptions by recording blood gas values in free-swimming tuna. We have developed techniques for capture, anaesthetization, instrumentation and recovery of tuna and for sampling dorsal and ventral aortic blood from animals swimming in a large doughnut-shaped tank. The results varied markedly from the above assumptions so we reinvestigated the blood gas properties of tuna blood and found, for kawakawa (*Euthynnus affinis*, Cantor), considerably different results from those obtained recently for bluefin (*T. thynnus*; Carey & Gibson, 1983) and albacore tuna (*T. alalunga*; Cech *et al.* 1984).

METHODS

Experiments were done on kawakawa, *Euthynnus affinis*, weighing from 0·9 to 2 kg, which were purchased from local commercial fishermen and maintained in outdoor tanks at 25 °C at the National Marine Fisheries Service Kewalo Research Facility.

For anaesthetization, a kawakawa was forced to swim into a plastic bag (complete method described in Kaya, Queenth & Dizon, 1984) containing oxygenated sea water and approximately $1\,\mathrm{gm\,l^{-1}}$ of the water-soluble fish anaesthetic, tricaine methanesulphonate (MS-222). The capture bag was held underwater until the fish stopped struggling. The fish was then rushed into the laboratory and placed dorsal side up in a cradle formed by suspending chamois leather between a vertical pair of plastic supports. Oxygenated sea water, with $0{\cdot}07$–$0{\cdot}1\,\mathrm{g\,l^{-1}}$ MS-222 to maintain anaesthesia, was recirculated over the gills through a tube placed in the mouth.

Catheterization of the dorsal aorta was done using a modification of the method described by Smith & Bell (1967) for salmonids. The animal was turned ventral side up and the gills were irrigated by backflushing oxygenated sea water through the opercular openings. The mouth was held open by retractors and either an 18 or 20 gauge Teflon catheter (5 cm long) was inserted into the aorta using an intravenous catheter placement unit. The placement unit consists of a stainless steel needle and hub, inside a Teflon catheter and hub. The catheter placement unit was filled with heparinized saline (10–30 i.u. ml^{-1}) and the inner steel needle was connected, *via* a coupling made from a 1-ml tuberculin syringe and a long length of saline-filled PE 160 tubing, to a blood pressure transducer. The needle and catheter were inserted through the skin at the point where the first gill arch joins the roof of the mouth (Fig. 1). To obtain the proper angle during insertion, the placement unit was then held approximately 0·5 cm medial to the 'V' formed on the side of the mouth by the premaxillary and dentary bones. The needle and catheter were then slowly pushed posteriorly until blood pressure was observed on a chart recorder. The needle hub was then held firmly and the catheter slid off the needle and advanced down the dorsal aorta. Blood pressure was carefully monitored at this time to ensure that the Teflon catheter remained in the blood vessel and that the tip did not become lodged against the vessel wall.

After the Teflon catheter had been advanced 2 or 3 cm down the dorsal aorta, the steel needle was quickly withdrawn and a male luer tip attached to a 1-m length of PE 160 tubing was inserted into the hub of the Teflon catheter. With practice this was performed with little blood loss. The catheter was then secured with a suture to the roof of the mouth and was brought out through the snout (Fig. 1) as described by Smith & Bell (1967).

It was necessary to enter the roof of the mouth at an angle, rather than in the midline, to avoid the large pharyngeal teeth overlying the dorsal aorta and bony knob projecting ventrally from the posterior end of the parasphenoid bone (see Gibbs & Collette, 1967, for a description of skeletal anatomy). An advantage of this procedure was that by positioning the placement unit near the 'V' formed by the premaxillary and dentary bones, an accurate angle for advancing the catheter was provided which ensured that the needle entered the aorta at the 'Y' formed by the combined efferent arteries from the first and second gill arches (Fig. 1).

The ventral aorta was also approached with the fish upside down. A placement unit was used to insert a Teflon catheter (18 or 20 gauge) approximately 1 cm anterior to the junction of the ventricle and bulbus arteriosus. This point was estimated using external markers as a guide. The body wall over the ventricle is stiff but over the extreme anterior end of the ventricle it becomes much more flexible. The placement unit was pushed through the skin in the midline, at a 45° angle to the body surface, approximately 0·5–1 cm anterior to the end of the stiff region of the body wall. The needle and catheter were advanced anteriorly until blood pressure was seen on the chart recorder. The needle was then held firmly and the Teflon catheter carefully advanced anteriorly along the ventral aorta. Once the catheter was in place, the needle was removed and a male luer connector on the end of PE 160 tubing plugged into the hub of the catheter. The whole system was then sutured to the body wall. At the conclusion of an experiment the location of the tips of the catheters in both dorsal and ventral aortae were checked *post mortem* (Fig. 1).

After catheterization, the animal was placed upright in the cradle and the catheters were sutured to the body wall just behind the dorsal fin. If recovery was to be effected the anaesthetic was slowly diluted until the animal started to make rhythmic body

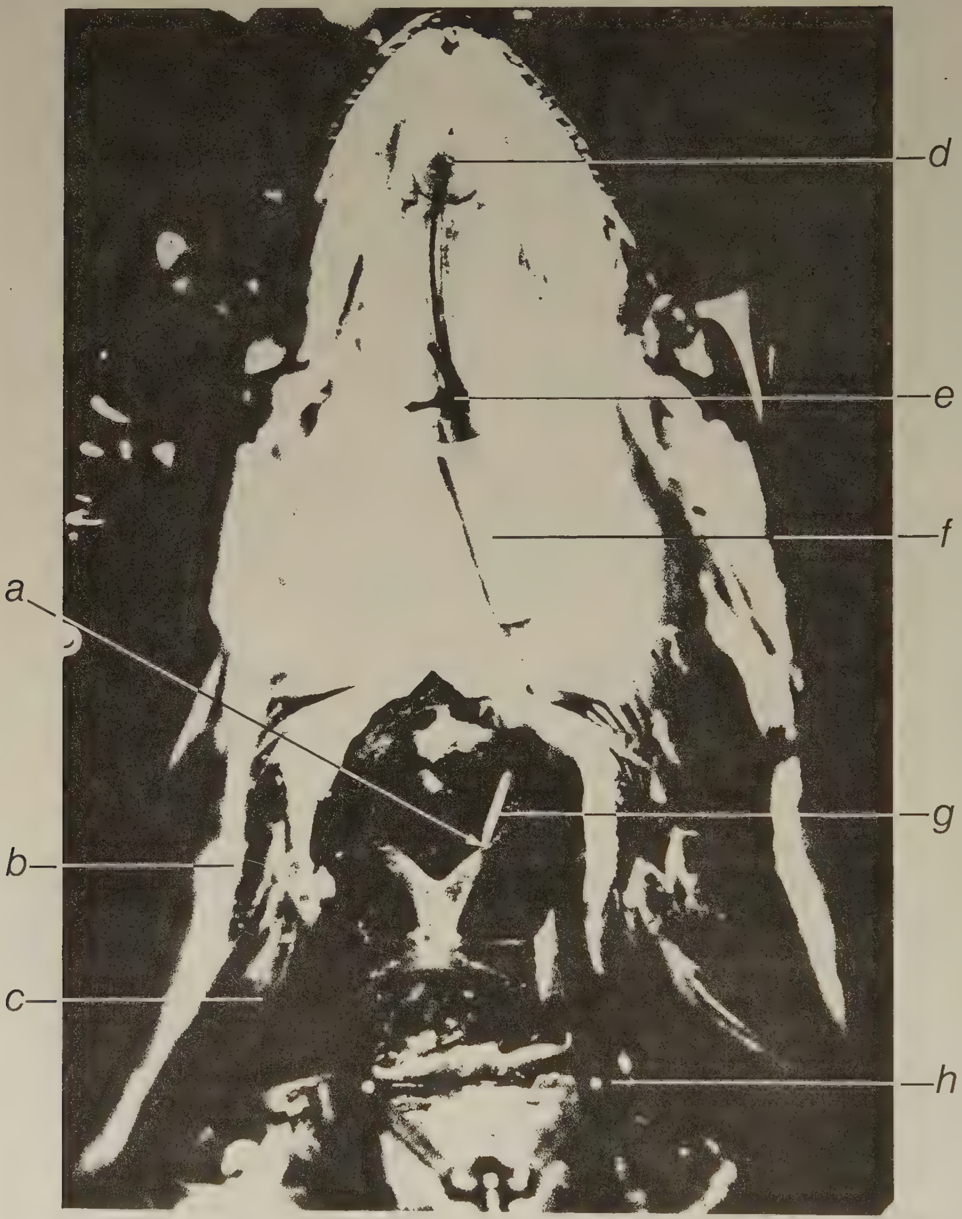

Fig. 1. Catheterization of the dorsal aorta in kawakawa, as revealed at *post mortem*. The lower jaw has been removed and the skin and muscle layers ventral to the dorsal aorta divided in the midline. The arrow shows the point of penetration into the efferent branchial artery. *a*, point of entry into gill artery; *b*, operculum; *c*, gills; *d*, flanged sleeve; *e*, tie to roof of mouth; *f*, catheter hub; *g*, Teflon catheter; *h*, retractors.

movements. Both catheters were plugged and the fish was rapidly transferred to a large doughnut-shaped tank (17·1 m i.d. and 17·8 m o.d.). Fresh sea water was pumped over the gills until the fish was able to swim on its own. Some fish swam laps of the tank and it was possible to get a fairly accurate assessment of swimming speed from these animals. Blood samples were taken simultaneously into syringes attached to the catheters, by an operator who ran around the tank keeping pace with the fish. After sampling, the catheters were flushed with heparinized saline and replugged. Survival was not good. Fish with dorsal and ventral aortic catheters succumbed within 3 h after the start of swimming. In three fish we only implanted a dorsal aortic catheter and these fish survived much longer, but all three died by 18 h after the end of the surgery. We are not sure whether the longer survival was due to less surgery or a decrease in the effort required to pull one cannula instead of two.

Other fish were not allowed to recover from anaesthesia. These animals were placed in a Perspex box, dorsal side up in the cradle, and were force-ventilated from a pump. A light level of anaesthesia was maintained throughout. The majority of these fish had only one catheter, located in either the dorsal or ventral aorta. Blood samples were taken from these fish and were used to construct O_2- and CO_2-combining curves.

Aliquots of blood (3–5 ml) were placed in tonometers (50 ml) which were shaken at 25 °C in a constant temperature bath. The blood was equilibrated for 20 min, a time found to be adequate, with humidified gases obtained from a gas mixing pump (Wösthoff, Bochum, W. Germany). Various mixtures of $P_{CO_2} = 0$, 2·54, 5·07, 11·5, 30·5 or 61·3 mmHg were made in both air and nitrogen and were stored in rubber tyres. P_{CO_2} tension was the same in a pair of tonometers. Blood samples were taken from each tonometer (one equilibrated with air + CO_2 and the other with $N_2 + CO_2$) and oxygen and carbon dioxide concentrations were determined using the methods of Tucker (1967) and Cameron (1971). The Tucker (1967) method was modified somewhat in that we used 100 μl of distilled water, equilibrated with pure oxygen at 25 °C, as a reference sample for determining oxygen concentration in 25 μl of whole blood. The cuvettes containing the oxygen and CO_2 electrodes were maintained at 40 °C to improve the response time of the electrodes and accuracy of the determinations. All solutions were also held at this temperature except the 100 % oxygenated distilled water. The P_{O_2} of this water, which was used as the reference sample, was measured using a Radiometer oxygen electrode at 25 °C. Oxygen equilibration curves were constructed using the mixing method (Haab, Piiper & Rahn, 1960; Edwards & Martin, 1966) but incorporating improvements suggested by Scheid & Meyer (1978). Haematocrits of the blood in the tonometers and of each sample after mixing were determined in duplicate. No haemolysis occurred, judging from the colour of the plasma in the haematocrit tube after centrifugation. Some blood was tonometered for long periods to determine if P_{50} changed with time. After 75 min of tonometry, P_{50} was the same as was obtained after 20 min. Eleven oxygen dissociation curves were constructed using the blood from five tuna at P_{CO_2} from 0 to 11·5 mmHg and 32 determinations of P_{50} were made on blood from nine fish. The presence of a Root effect means that at a given P_{O_2} blood will carry less oxygen as the

P_{CO_2} increases. Hence, in fish blood, the P_{50} obtained at various P_{CO_2} levels does not represent similar concentrations of oxygen. As this reflects the situation *in vivo*, no attempt was made to correct values from the mixing method for the Root effect. CO_2-combining curves were constructed also using the blood from six fish; the blood of two of these had been used in determinations of oxygen-combining properties. The Root effect was measured in blood from six fish, although each fish was used for only a single determination.

Blood gas tensions and pH were measured using Radiometer electrodes, in cuvettes thermostatted at 25 °C, and connected to Radiometer PHM 71 Mk 2 or Radiometer PHM 73 gas monitors. The pH electrode was calibrated using precision buffer solutions and the gas electrodes with mixtures obtained from the gas mixing pump, although the zero calibration on the oxygen electrode was checked periodically using an alkaline sulphite solution (S4150, Radiometer, Copenhagen). The environmental temperature of the kawakawa was 25 °C so as to simulate the effects of the blood being warmed in the retial system, dorsal aortic blood samples, from three fish, were drawn into glass syringes and injected into cuvettes held at 35 °C and analysed in a blood gas system maintained and calibrated at 35 °C. A stable reading was obtained after 2 min. The values for the warmed blood were compared with values obtained at 25 °C using freshly drawn blood analysed in the blood gas system held and calibrated at 25 °C.

In the text, all values are given as means ± one S.E.M., (N), where N = number of observations. Regression analyses were performed on a computer using the data analysis package, ‘S’, for UNIX operating systems (Becker & Chambers, 1984).

RESULTS

In vivo *observations*

Blood gas values and pH of blood from tuna swimming at speeds from 1·8 to 2·9 body lengths s^{-1} are given in Table 1. Dorsal aortic blood was always more alkaline than ventral aortic blood although in one case the difference was quite small (tuna no. 1, Table 1). Nevertheless, this contrasts with our extrapolation of Cech *et al.*'s (1984) data which indicated that dorsal aortic blood would be more acid than ventral aortic blood. Ventral aortic P_{O_2} never exceeded 16 mmHg, while dorsal aortic P_{O_2} was always below 100 mmHg and in two of the three tuna that only had a dorsal aortic cannula and survived 18 h post-operatively, dorsal aortic P_{O_2} was below 42 mmHg (tuna nos 7 and 8, Table 1). P_{CO_2} in the dorsal aorta varied from 3·7 to 7 mmHg but there was no apparent relationship between dorsal aortic P_{O_2} and P_{CO_2}.

Warming dorsal aortic blood sampled from three free-swimming kawakawa by 10 °C, from 25 to 35 °C in a closed system, caused P_{O_2} to increase by 25 % ± 14 % (9) and P_{CO_2} to more than double [increase = 105·7 % ± 6·4 % (9)]. The P_{O_2} of the freshly sampled blood varied from 40 to 102 mmHg at 25 °C and P_{CO_2} varied from 2·9 to 5·1 mmHg. Dorsal aortic blood pH fell by, on average, 0·15 ± 0·01 (9) units when blood was warmed by 10 °C.

Table 1. *Blood gas tensions and pH in blood sampled from free-swimming tuna* Euthynnus affinis

	Ventral aorta						Dorsal aorta			
Tuna no.	P_{O_2} (mmHg)	P_{CO_2} (mmHg)	pH	Hct (%)	Fork length (cm)	Swimming speed (body lengths s^{-1})	P_{O_2} (mmHg)	P_{CO_2} (mmHg)	pH	Hct (%)
1	14	8·9	7·57	29	43	SNR	56·4	5·2	7·59	29
2	16	5·8	7·68	—	42	SNR	—	—	—	
3	12·7	10·7	7·66	28	37·5	2·9	68·7	7	7·80	24
4	11·7	8·6	7·70	42	45	1·8	67·4	5·4	7·76	35
5	8·5	8·9	7·61	44	44	2·27	44·6	6·9	7·68	39
6	12	7·3	7·73	32	47	1·8	91·7	4·2	7·8	34
7	—	—	—	—	37	SNR	41·7	4·1	7·74	36
8	—	—	—	—	36	SNR	34·5	4·2	7·83	43
9	—	—	—	—	38	SNR	88	4·7	—	28
10	12·5	6·2	7·60	37	37	SNR	52	3·7	7·76	37
	12·5 ± 0·9 (7)	8·07 ± 0·65 (7)	7·65 ± 0·02 (7)	35·3 ± 2·75 (6)			62·7 ± 5·92 (9)	5·05 ± 0·4 (9)	7·77 ± 0·04 (8)	33·8 ± 1·97 (9)

SNR = fish swimming but speed not recorded.
Number of fish given in brackets.

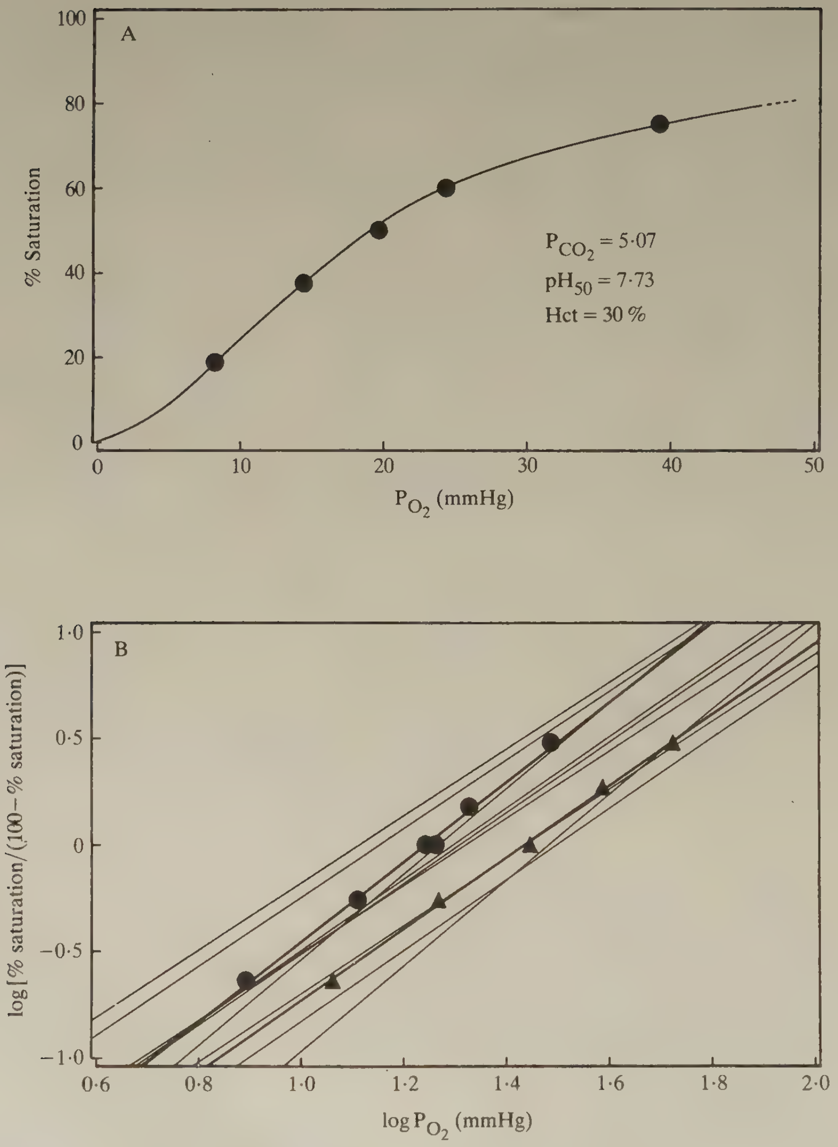

Fig. 2. (A) A blood oxygen dissociation curve of kawakawa whole blood (Hct = 30 %) at 25 °C and $pH_{50} = 7{\cdot}73$. The blood was equilibrated with gas mixtures containing 5·04 mmHg P_{CO_2}. The curve was fitted by eye. (B) Hill's plots of the 11 oxygen dissociation curves determined in this study. Data points are only shown for the two heavy regression lines.

In vitro *observations*

Oxygen-combining properties of kawakawa blood

Dissociation curves for the blood were sigmoid (Fig. 2A) with a mean Hill's number of 1·72 ± 0·05 for the eleven determinations (Fig. 2B). Hill's numbers varied from 1·57 to 2·0 over a pH range (at the P_{50}) of 7 to 8, but there was no relationship between the value of Hill's number and pH. At full saturation, oxygen concentration in the blood varied with haematocrit. This relationship is expressed by the equation:

$$\text{Oxygen (mmol l}^{-1}\text{)} = -0{\cdot}7 + 0{\cdot}27\,\text{Hct\%}\ (r^2 = 0{\cdot}76).$$

P_{50} increased with a decrease in pH of the blood, caused by changing P_{CO_2}, from 10·1 mmHg at pH = 7·95 to 41·5 mmHg at pH = 7·13. Over the range of pH values encountered in free-swimming tuna (pH 7·57–7·83), the P_{50} varied from 30·9 to 13·7 mmHg, with an average value of 21 ± 1·75 mmHg (8). The oxygen concentration of the blood fell (Root effect) with an increase in P_{CO_2} from 0 to 61·3 mmHg, by −0·64 ± 0·1 % mmHg $P_{CO_2}^{-1}$ (6) ($r^2 = 0{\cdot}9$), where the oxygen concentration at $P_{CO_2} = 0$ mmHg was taken as 100 %.

The Bohr coefficient, obtained from a plot of log P_{50} *versus* pH, was −0·59 ± 0·046 (30) ($r^2 = 0{\cdot}85$) (Fig. 3). The Bohr coefficient increased to −0·83 ± 0·23 (10) ($r^2 = 0{\cdot}61$) over the more restricted pH range from 7·55 to 7·85, which encompassed the pH values obtained in free-swimming animals.

Blood from a single fish which struggled violently just before sampling had a pH around 7 even after 20 min equilibration with a gas mixture without CO_2. Two determinations of P_{50} on this blood fell considerably below the line describing the CO_2-induced Bohr effect (▲ in Fig. 3). Unfortunately, lactate concentration was not measured but if the low pH was due to lactacidosis then these data indicate that CO_2-induced and metabolic acid-induced Bohr coefficients could be different.

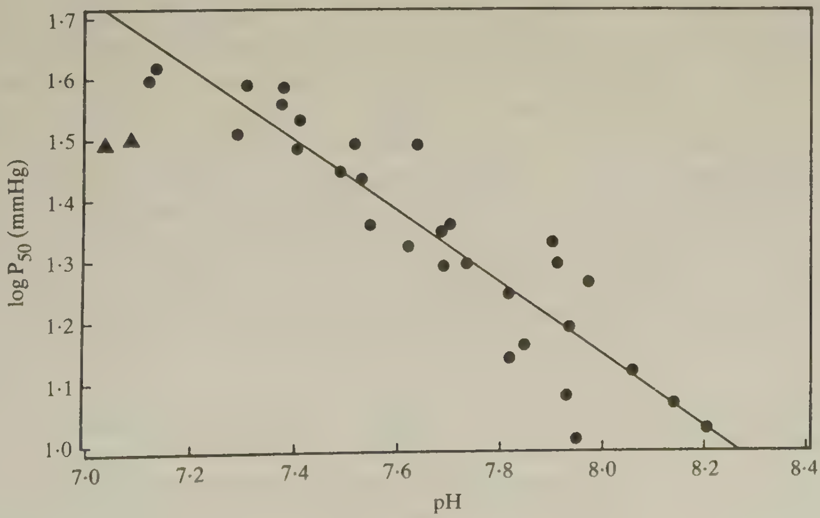

Fig. 3. Plot of logP_{50} *versus* pH for determining the CO_2-induced Bohr coefficient of kawakawa whole blood at 25 °C. Two points (▲) were obtained from blood in which pH was low even though the equilibrating gas was without CO_2. These points were not included in determining the CO_2-induced Bohr coefficient.

Carbon dioxide-combining properties of kawakawa blood

The relationship between P_{CO_2} and CO_2 concentration for whole blood, with haematocrits in the range from 29 to 36% (average 31·5%), is shown in Fig. 4A. At any given level of P_{CO_2}, deoxygenated blood had a higher concentration of CO_2 than oxygenated blood, although the difference in concentration was unchanged over a P_{CO_2} range from 2·5 to 30·5 mmHg. A 'buffer curve' was obtained by plotting the relationship between pH and $\log P_{CO_2}$ for blood samples with haematocrits from 25 to 35% (Fig. 4B). The slope of the relationship for deoxygenated blood [$-0{\cdot}611 \pm 0{\cdot}04$ (9) ($r^2 = 0{\cdot}97$)] appeared steeper than that for oxygenated blood [$-0{\cdot}5 \pm 0{\cdot}04$ (9) ($r^2 = 0{\cdot}96$)], but the difference between the slopes was not significant at the 5% level.

DISCUSSION

Predicted values of blood gas tensions in dorsal and ventral aortae of tuna based on published values of blood gas chemistry are at variance with our measurements in free-swimming kawakawa. Apart from errors in measurement or interpretation, the only possibility which could explain these discrepancies is marked interspecific variations in the oxygen- and CO_2-combining properties of tuna blood. In this respect, our recordings of oxygen- and CO_2-combining properties of kawakawa blood substantiate the measurements we obtained from free-swimming fish. For instance, the Bohr coefficient is less than $-0{\cdot}6$ and in every instance dorsal aortic pH was more alkaline than that in the ventral aorta. Ventral aortic P_{O_2} was, on average, 12·5 mmHg, which was well below the mean value for P_{50} observed over the range of pH encountered in free-swimming fish.

Dorsal aortic P_{CO_2} was high and, in fact, is perhaps the highest yet reported for free-swimming teleosts (Stevens & Randall, 1967; Holeton, Pawson & Shelton, 1982; Boutilier, Aughton & Shelton, 1984). The high arterial P_{CO_2} may explain, in part, why no reverse temperature effect on blood oxygen dissociation was observed when dorsal aortic blood was warmed from 25 to 35°C. Even so, a much reduced reverse temperature effect was expected because Cech *et al.* (1984) reported that the effect is diminished and reverts to a more typical form between 30 and 35°C in albacore blood. In their environment and in the holding tanks, our tuna can live quite happily in the absence of any advantage conferred by reversed thermal effects. It may be that the low dorsal aortic P_{O_2} observed in free-swimming animals renders this effect unnecessary or, more likely, that the claimed advantage of this effect in ensuring adequate muscle oxygenation has been overstated (see Carey & Gibson, 1983).

In most vertebrate bloods there is a difference in CO_2 concentration between oxygenated and deoxygenated blood, at a given P_{CO_2}. This difference increases with increasing P_{CO_2}. Also, deoxygenated blood is more alkaline than oxygenated blood at any given P_{CO_2}, and this pH difference is constant over a wide range of P_{CO_2} values. These differences are a reflection of changes in the properties of haemoglobin on oxygenation or deoxygenation. Hence, the CO_2-combining properties of kawakawa blood are unusual in that the CO_2 concentration difference between oxygenated and deoxygenated blood does not increase with P_{CO_2} while the pH difference is reduced with increasing P_{CO_2}. As these differences are dependent on oxygen combining with haemoglobin, the unusual properties of kawakawa blood are probably the result of the Root effect.

Our method of looking at the buffering properties of tuna blood should also be mentioned. In the light of recent quantitative analyses of acid–base balance

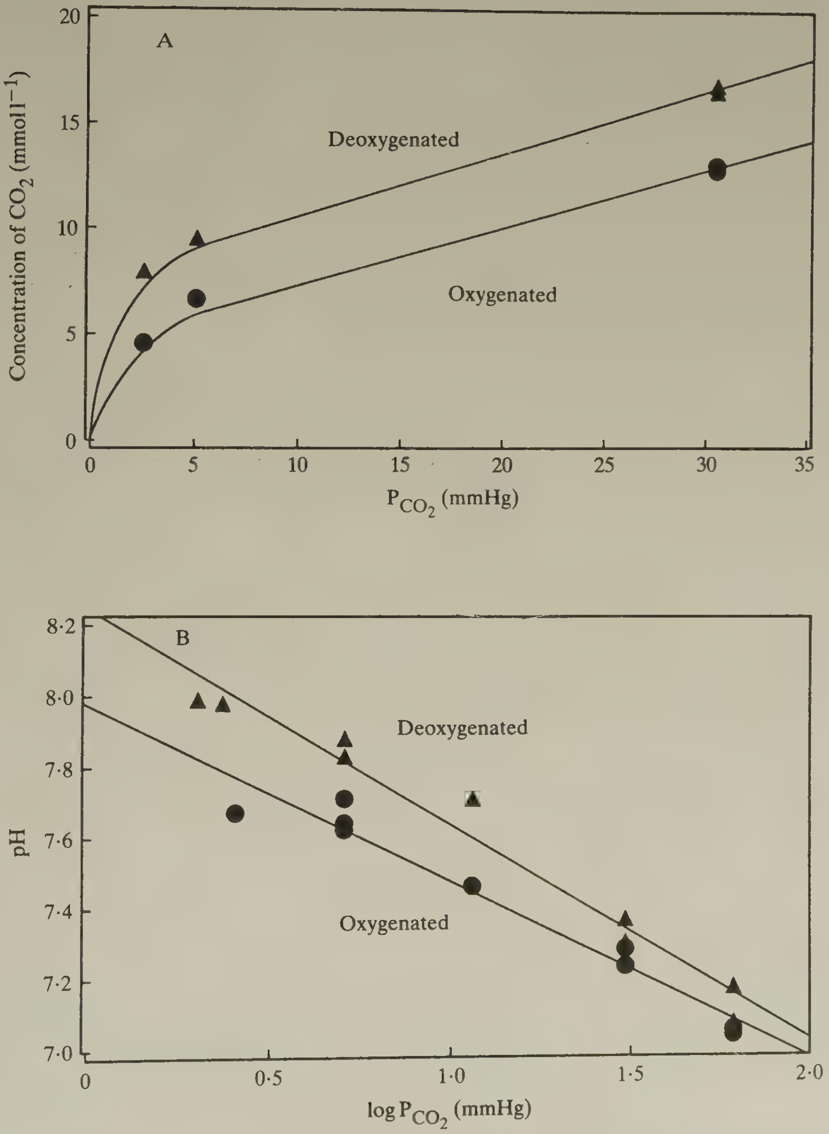

Fig. 4. (A) CO_2-combining curve for air-saturated and deoxygenated blood of kawakawa at 25°C. Curves fitted by eye. (B) 'Buffer curves' of air-saturated and deoxygenated kawakawa whole blood displayed as the relationship between pH and log P_{CO_2}.

(Stewart, 1983) it seems more rational to analyse buffer properties with the independent variable (P_{CO_2}) on the abscissa rather than the ordinate. The slope of the relationship, pH *versus* $\log P_{CO_2}$, for tuna blood falls between $-0{\cdot}5$ (oxygenated) and $-0{\cdot}61$ (deoxygenated) which is in the same range as values obtained from elasmobranchs and other teleosts (Albers & Pleschka, 1967; Cameron & Randall, 1972; Root, 1931; Weber, Wells & Rossetti, 1983).

In the pH range 7 to 8 we found that the variation in Hill's number, from 1·57 to 2·0, was not related to pH. Hill's equation is theoretically incorrect, and is usually replaced by the Adair intermediate compound equation, but it is still a convenient and useful way to compare physiological data. Given the above proviso, the value for Hill's number of 1·1 obtained by Cech *et al.* (1984) for albacore blood is strikingly different from that for kawakawa blood. Finding a hyperbolic blood curve (Hill's number = 1) in an extremely active and highly aerobic animal like tuna is quite unexpected. Tuna are warm-bodied and are claimed to consume oxygen at the same rate as similarly sized mammals (Stevens & Carey, 1981), so a sigmoid dissociation curve would be expected (Haldane & Priestley, 1935; Riggs, 1970) and this has been confirmed by the present observations on kawakawa.

A theoretical analysis based on morphometric observations of the gills (Hughes, 1978, 1984) and estimates of gill water flow (Stevens, 1972), suggests that P_{CO_2} in dorsal aortic blood of tuna will be low (Rahn, 1966). Obviously this was not the case (Table 1). The fact that dorsal aortic P_{O_2} was also low implies that, at least at swimming speeds of 1·8–3 body lengths s^{-1}, efficacy of gas transfer is compromised. Certainly it would be most valuable to obtain data from tuna swimming at higher speeds; observations on the scombrid, *Scomber scombrus*, indicate that dorsal aortic P_{CO_2} falls when swimming speed increases (Boutilier *et al.* 1984). The fall in P_{CO_2} serves to minimize the effects of increasing lactacidosis on dorsal aortic pH. Whether dorsal aortic P_{O_2} would increase and P_{CO_2} fall at higher swimming speeds in tuna is not known but it is an interesting avenue for future research.

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EVIDENCE FROM STRANDINGS FOR GEOMAGNETIC SENSITIVITY IN CETACEANS

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SUMMARY

We tested the hypothesis that cetaceans use weak anomalies in the geomagnetic field as cues for orientation, navigation and/or piloting. Using the positions of 212 stranding events of live animals in the Smithsonian compilation which fall within the boundaries of the USGS East-Coast Aeromagnetic Survey, we found that there are highly significant tendencies for cetaceans to beach themselves near coastal locations with local magnetic minima. Monte-Carlo simulations confirm the significance of these effects. These results suggest that cetaceans have a magnetic sensory system comparable to that in other migratory and homing animals, and predict that the magnetic topography and in particular the marine magnetic lineations may play an important role in guiding long-distance migration. The 'map' sense of migratory animals may therefore be largely based on a simple strategy of following paths of local magnetic minima and avoiding magnetic gradients.

INTRODUCTION

The problem of how migratory animals find their way has been a subject of curiosity and investigation for centuries. Although it is known that a variety of organisms from butterflies to birds regularly take highly accurate, long-distance journeys of extensive duration, how they navigate or pilot remains a mystery. Within the last 35 years a plethora of sensory modalities has been identified in homing and migratory birds which to date includes the use of a sun compass (Kramer, 1952), a star compass (Sauer, 1957), skylight polarization patterns (Kreithen & Keeton, 1974), odour (Papi, Fiore, Fiaschi & Benvenuti, 1972), infra-sound (Kreithen & Quine, 1979), ultra-violet light (Kreithen & Eisner, 1978) and magnetism (Keeton,

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1972; Walcott & Green, 1974). Many of these cues, however, are not available to aquatic animals and yet they also can make highly accurate journeys across apparently featureless seas.

The use of geomagnetic cues for orientation and navigation is perhaps the most surprising discovery to be made in this field so far, principally because it implies the presence of a previously unknown type of sensory receptor capable of transducing very weak features of the geomagnetic field to the nervous system (Kirschvink & Gould, 1981). However, geomagnetic sensitivity has been demonstrated in bacteria (Blakemore, 1975), bees (e.g. Gould, 1980; Walker & Bitterman, 1985), birds (e.g. Keeton, 1972; Walcott & Green, 1974; Walcott, 1978) and fish (Kalmijn, 1974; Walker, 1984) and the recent discovery of chains of biogenic magnetite crystals within many of them provides at least a theoretical basis for understanding how a magnetic sense might operate (e.g. Kirschvink & Gould, 1981; Kirschvink & Walker, 1985; Yorke, 1979, 1981; Blakemore & Frankel, 1981; Walker, Kirschvink, Chang & Dizon, 1984). One problem with the behavioural aspects of this work, however, is that most responses to geomagnetic stimuli are weak and difficult to observe in laboratory settings; this led Griffin (1982) to assert that perhaps organisms had no useful sensitivity to the geomagnetic field. Alternatively, a geomagnetic sense, which clearly should be very useful, might only be expressed under the influence of an unknown set of environmental conditions. Work on pigeons (Keeton, 1972; Wiltschko, 1983) indicates that several other sensory modalities supersede the magnetic sense when they are available.

For the biological reader, it is worth briefly comparing here the difference between the aeromagnetic (e.g. measured from low-flying aircraft) characteristics over the continents and those over most of the oceans; this distinction is highly relevant to the problem of oceanic navigation or piloting and leads to the suggestion that following or keeping track of local magnetic minima (rather than the maxima, for example) is not a bad strategy for long-distance pelagic navigation and could arise through natural selection. Continents are built up of complex assemblages of igneous, metamorphic and sedimentary rocks, which can possess large regional variations in their mineral and chemical contents. The most important variable which influences the surface magnetic field is the concentration of *coarse-grained* magnetite (Fe_3O_4). In magnetite crystals larger than about 20 μm, the magnetic moment will shift easily in the geomagnetic field and yield a strong magnetic moment aligned parallel to the local field. Rocks which contain large magnetite grains will, therefore, have higher than average magnetic susceptibilities. Particles of this size are common in most igneous and metamorphic rocks, and whenever a body of this sort intrudes into something with a lower magnetite concentration a strong positive magnetic anomaly flanked by more diffuse magnetic lows will typically result. Continents appear in general as magnetically 'flat' areas with superimposed 'hills' and a few 'holes'; the false-perspective maps of the iron-mine magnetic anomaly in Rhode Island shown by Gould (1980) and Kirschvink (1982) are good examples of this. In these places with a locally intense field the regional geomagnetic characteristics are unpredictable, and a migratory or homing animal is well advised to seek a magnetically 'flat' place before using subtle features of the magnetic field as a reference. Pigeons seem to do this when released at magnetic anomalies (Walcott, 1978; Wagner, 1983).

This situation contrasts starkly with that seen over the world oceans, however. In the late 1950s and early 60s it was first realized that the oceanic crust has a totally different magnetic character, composed of long bands of magnetic highs and lows (Mason, 1958; Mason & Raff, 1961), aligned parallel to the axes of mid-oceanic ridges. Observations of this sort led directly to the Vine–Matthews–Morley hypothesis (Vine & Matthews, 1964; see also Glenn, 1982) which proposed that new ocean floor is continuously created at the mid-oceanic ridges through the process of sea-floor spreading (Hess, 1962) and that periodic reversals in the global geomagnetic field give rise to the marine magnetic stripes. As the new basaltic crust is injected and cools at the spreading ridge, *fine-grained* magnetite drops through its Curie temperature and permanently records the local geomagnetic field direction. The remanent magnetization produced in this fashion is stable over long intervals of geological time, and the alternating normal and reversely magnetized blocks produce anomalies at the ocean surface in most regions with amplitudes ranging from a few hundred to thousands of nanotesla (nT), compared with a geomagnetic total strength ranging from 29 000 nT at the equator to over 80 000 nT near the poles.

The Vine–Matthews–Morley hypothesis was dramatically confirmed in 1966 when it became apparent that the magnetic reversal sequence as worked out from dated volcanics on land (Cox, Dalrymple & Doell, 1967) and in deep-sea cores (Opdyke, Glass, Hayes & Foster, 1966) matched perfectly the symmetrical magnetic anomalies centred over oceanic ridges (Vine, 1966). Subsequent work has extended the geomagnetic reversal time scale back to about 160 million years and now permits the geological and tectonic history of almost all oceanic basins to be worked out in detail by simply towing or flying magnetometers over them. The Vine–Matthews–Morley hypothesis is therefore the cornerstone of modern plate tectonic theory, provides the mechanism for continental drift and is by far the single most important new concept in the earth sciences since the early 1800s (Glenn, 1982).

Of potentially great interest to the problem of animal migration and navigation is the fact that most of these marine magnetic lineations in the major ocean basins are aligned in a North–South fashion, a fortuitous result from the geometry of the spreading ridges which formed after the break-up of the continent Pangea during Mesozoic time. An animal could therefore use these lineations by counting or following minima to keep track of relative *longitude* during long migrations if it were sensitive enough to the magnetic field, while the smooth North–South variation of magnetic *inclination* would provide unambiguous *latitudinal* position. Depending on the age, depth and latitude of the sea floor, the magnitude of these anomalies can range from a few hundred to several thousand nanotesla – figures which are also well within the sensitivity range inferred for homing pigeons and honey bees and also well within the theoretical limits for magnetite-based magnetoreception (Kirschvink, 1979; Kirschvink & Gould 1981; Yorke 1981; Kirschvink & Walker, 1985).

The use of cetacean stranding positions in a test of a geomagnetic navigation or piloting hypothesis, as done by Klinowska (1983) and adopted here, may at first seem to be a strange approach. Although something is obviously wrong with a living marine mammal that swims onto the shore, it *is* attempting to move somewhere, and it seems likely that cetaceans are more apt to strand in areas unfamiliar to them. For this reason stranding records probably contain more information about the sensory cues used during long-distance migration than any other set of positional data collected for them, with the exception of radio tracking studies (Mead, 1979). We wish to make it clear that our goal is *not* to test hypotheses about *why* cetaceans strand. Our goals are to test the hypotheses that: (1) cetaceans have a sensitivity to weak geomagnetic stimuli, and (2) that geomagnetic cues may influence their distributional patterns in a predictable manner. For this purpose, we use the stranding records merely as a subset of the positions of all living cetaceans.

Our approach for testing these geomagnetic sensory hypotheses therefore begins by noting that stranding positions within a magnetic 'valley' have an easily examined attribute: the coastline adjacent to a stranding should have higher intensity than does the stranding site. Our results indicate that, in most cetacean species, live strandings do indeed tend to happen at magnetically lower-than-average places along the coastline, confirming in a general way the hypothesis of Klinowska (1983). However, there are a few clear counter-examples which suggest that the situation in some species is more complex than this, and on occasion they may use other features of the geomagnetic field (e.g. magnetic highs, gradients, etc.) for guidance.

METHODS AND DATA

We used the extensive stranding data available for the eastern U.S. coast, which is one of the best areas for investigating the relationship between cetacean strandings and the geomagnetic field because of the availability of three large computerized data sets. First, the Smithsonian Institution in Washington, D.C., has maintained a catalogue of cetacean strandings in which the geographical locations of these events are either listed or can be determined using the given place names and detailed topographic maps. Second, the U.S. Geological Survey has conducted an aeromagnetic survey of the U.S. East-coast continental margin with dense coverage from Cape Canaveral in Florida to Cape Cod in Massachusetts. These data are available on magnetic tape in gridded digital format as discussed below and shown as a colour image on Fig. 1A,B: they constitute one of the most complete and extensive aeromagnetic data sets available for any portion of the globe. Finally, any test of stranding hypotheses necessarily depends on the geometry of the coastline itself; it must be known accurately to be of any use. For the analysis discussed in this paper we used the high-resolution digital world outline from the plotting package, SUPMAP, developed by the U.S. National Center for Atmospheric Research (NCAR).

Stranding data

The Marine Mammal Program of the Smithsonian Institution maintains a large data-base which contains records of stranding events occurring along the U.S.

coastline. This file contains information on strandings gleaned from records kept on specimens and data archived in museums, from reports in 'grey literature' and mass media, from published scientific literature, and from the SEAN monthly publications (Smithsonian Scientific Event Alert Network). Through the cooperation of the leader of the Marine Mammal Program, Dr James Mead, a sub-set of data was provided for us which included all strandings, from which we obtained records of live stranding events.

Geographical information provided in each record was of varying degrees of completeness. Some records contained geographical coordinates, others contained only beach or town names. We reviewed each record, and for those without coordinates we provided a best estimate of latitude and longitude (to the nearest minute) using National Ocean Survey marine charts whenever possible. This phase of the study was performed at the NMFS facility in La Jolla, and at this time no information on the magnetic intensity at the various coast locations was on hand. Although there was some degree of subjectivity associated with determining coordinates for stranding events, no systematic bias was possible without magnetic information. Besides geographical information, the species, number of animals involved, state of preservation (1 = live, 2 = freshly dead, 3 = slightly bloated, etc.), and a subjective measure of the degree of accuracy of a stranding location were included. Only locations known to within 1′ were used in our analyses. Table 1 gives a list of species for which we were able to find live stranding events with highly reliable locations within the area of the aeromagnetic survey discussed next.

Magnetic data

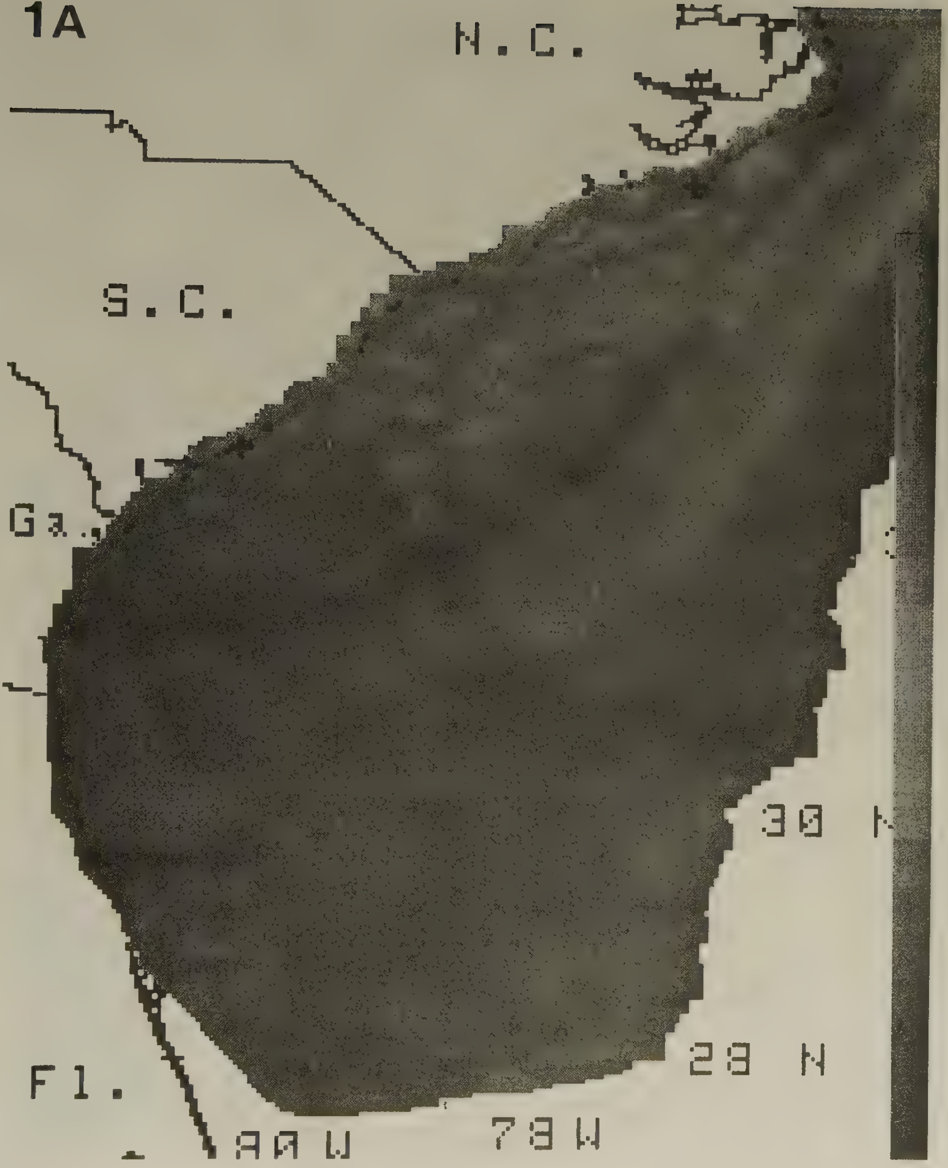
The aeromagnetic survey of the U.S. Atlantic Continental Margin (Grim, Behrendt & Klitgord, 1982) is at the heart of this study; we obtained these data from the NOAA Geophysical Data Center on magnetic tape in high-density gridded digital format covering the areas shown on Fig. 1A,B. Each data point represents 0·036° spacing in latitude and longitude, or approximately a 4-km square. Flight tracks began between 5 and 20 km inland and continued out to the 2000-m isobath, and were generally spaced of the order of 2·5–5 km apart with altitudes between 300 and 450 m. The position accuracy was estimated to be better than ±1 km using LORAN C, VLF and doppler-radar. Data from these flights were fitted by a method of least-squares to this gridded surface and corrected for diurnal variations. Grim *et al.* (1982) also subtracted the 1965 International Geomagnetic Reference Field (IGRF) and added a baseline of 52 000 nanotesla (nT). We removed 50 790 nT from this baseline to permit the residual field values to fit in 2 bytes of memory (Integer *2) on our VAX 11/780 computing system. (All of the analyses used here depend only on the relative field difference between pixels, so the subtraction of this constant has no effect on the overall analysis.)

We choose to represent this information as the colour images shown here in Fig. 1A,B. The gridded magnetic data have been mapped onto a 500×500 array of pixels (picture elements), with the colour at each pixel representing the average field value for the 0·036° square (bright yellow areas indicate high magnetic field values and dark blue areas are low values with 256 shades of resolution covering the 2000 nT range of data values shown on the colour step wedge). Fig. 1A,B also shows the image of these data with a light background and the outline of North America and state boundaries superimposed. This method of representing the data avoids most of the visual confusion which results from attempting to plot geographical locations on a false-perspective, contoured surface as used previously (Gould, 1980; Kirschvink, 1982).

One problem with these data, however, is a long-distance shift in the average baseline value which increases by as much as 600 nT from South to North (W. Heinze, personal communication, 1984). The problem either lies in the 1965 IGRF correction to the raw data (it might not properly remove some of the non-dipole components of the main geomagnetic field) or there may be a thin zone containing native iron near the base of the crust in this portion of the Atlantic (D. Strangway, personal communication, 1985). As discussed later, this problem makes it difficult to conduct one of the more intuitive statistical tests.

Fig. 1. (A) and (B). Images of the aeromagnetic survey data for the Atlantic Continental Margin from Cape Canaveral, Florida, through Cape Cod, Massachusetts, with the coastline, political boundaries and live stranding events superimposed. The USGS aeromagnetic data are supplied in a gridded, digital format with each point or pixel (picture element) representing the residual magnetic field value after removal of the IGRF in a square 0·036 degrees in both latitude and longitude. In both A and B, the value of the residual magnetic field in each pixel is indicated by the shade of colour ranging smoothly (256 shades) from dark blue to bright yellow, with blue and yellow respectively indicating magnetic lows and highs. Each image has a 20-step colour wedge which shows the relative intensity calibration in 100 nanotesla (nT) steps across the entire 2000-nT variation in the magnetic data set. (This variation is about 2 % of the total field strength before removal of the IGRF.) A one-degree latitude and longitude grid has been lightly superimposed on the magnetic data, and areas outside the boundaries of the aeromagnetic survey are shown in white. All live cetacean stranding locations referred to in this study are plotted in red, with the position of large mass stranding events (> 30 individuals) shown by the large red + marks, smaller mass strandings (between three and thirty individuals) by smaller + marks, and events of one or two individuals as single red pixels. Outside of the aeromagnetic survey area, the position of the coastline and state boundaries are plotted in green. Within the survey area, the position of the coastline can be followed both by the location of the stranding events and by a light reddish tint which has been added to the otherwise blue-yellow pixels. Abbreviations of state names and a few latitude and longitude coordinates are shown in black for reference. (A) Southern area from Cape Canaveral in Florida through Cape Hatteras in North Carolina. Several prominent magnetic minima which are branches of the East-coast magnetic anomaly cross the coast in the Florida–Georgia segment of this image, and are associated with mass-stranding events. These may be migration routes at sea, and sediments near their intersection points along the coast should have abundant whale-bone fossils as a result of numerous mass stranding events during periods of normal geomagnetic polarity. (B) Northern area from just north of Cape Hatteras in North Carolina through Massachusetts. The boomerang-shaped bright-yellow stripe running through the centre of the map is the East-coast magnetic anomaly, and south of this several faint marine magnetic lineations can be seen. The bright-yellow spot on the eastern margin of the image is the magnetic anomaly of a seamount.

1A


N.C.
S.C.
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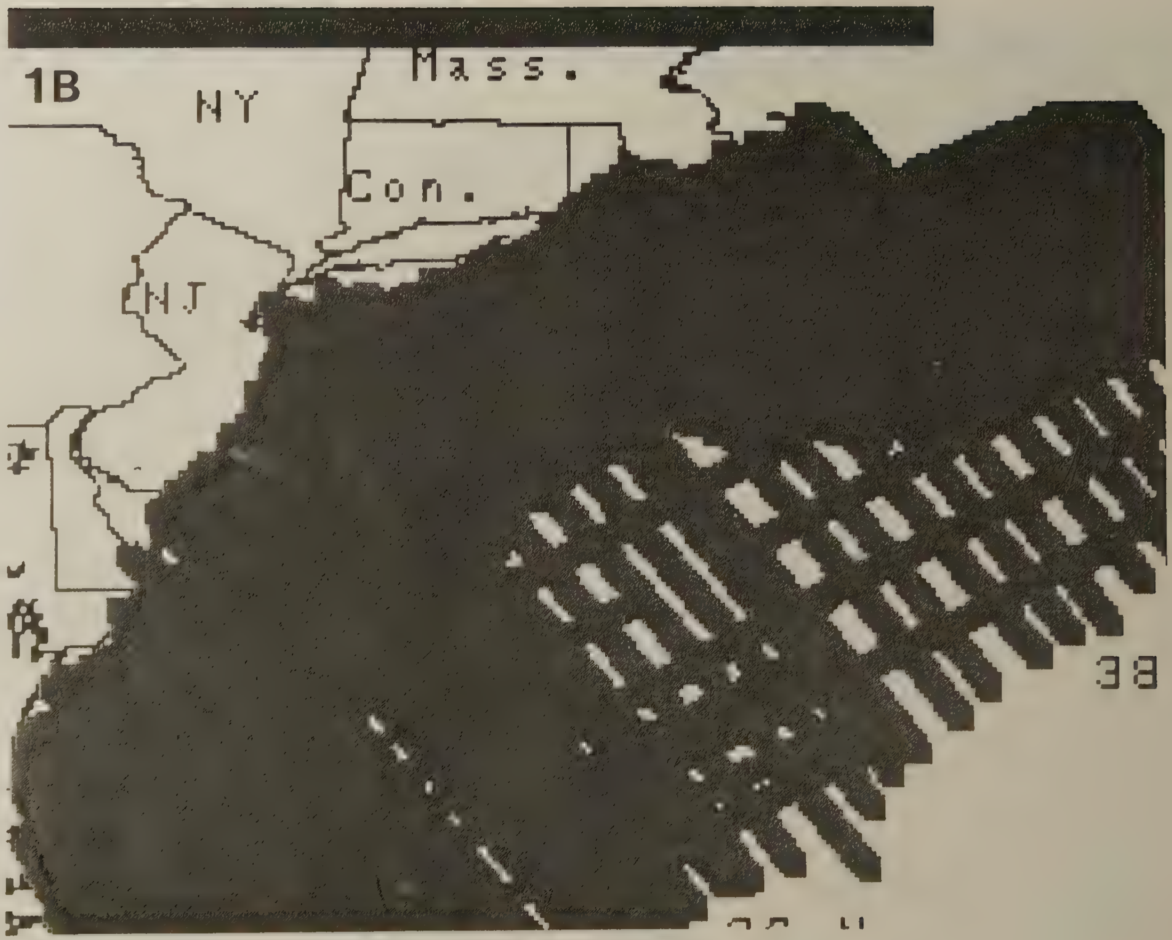
30 N
28 N
80 W
78 W


1B
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Mass.
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38

Coastline data

The third major data set, an accurate digital representation of the coastline within the aeromagnetic survey area, is needed in this study for two reasons. First, gross errors in the cetacean stranding file were easily found by checking their pixel assignments against those of the coastline. The position of any stranding event which 'happened' far out at sea or inland was suspect and was re-checked by consulting the geographical position of the stranding in the Smithsonian listing. Secondly, cetaceans live-strand along the *coast*, and by using the set of all coastal points we reduce the statistical problem to a one-dimensional analysis. The two-dimensional case is more complex, and inappropriate as it would incorporate off-shore and inland magnetic data where cetaceans do not strand.

We used the world digital outline data set obtained from the NCAR graphics program, SUPMAP, which contains high-resolution coastal outline positions accurate to 0·001° in both latitude and longitude. All pixels within the 500×500 map area which contain segments of the coastline were identified and numbered in consecutive order as they were encountered, beginning at Cape Canaveral in Florida and continuing to Cape Cod in Massachusetts. A total of 1364 distinct pixels was located in this search within the boundaries of the aeromagnetic data set, including offshore and barrier islands. Of these, 283 are included two or more times in the full set of 1692 due to meandering of the coastline. During this search, the total shoreline distance within each consecutive coastal pixel was also measured to provide the distance function needed for the statistical analysis discussed below.

Due to the presence of islands and rivers, the coastline is not one continuous stretch. In a few places it also wanders in and out of the area covered by the aeromagnetic survey and jumps onto and off islands. These discontinuities result in a total of 40 coastal segments within which the magnetic field is known continuously. The gaps between them imply that they must be treated as discrete entities in procedures discussed below; 23 of them contain one or more stranding events, and the 17 segments with no strandings are usually small islands or the inland side of brackish-water inlets. Segments without strandings were not used for any analysis discussed here.

Fig. 2 shows the plot of the residual total field values as a function of shoreline pixel number, and the histogram underneath it indicates the position and number of stranding events within each pixel. The locations of mass stranding events ($N \geqslant 3$) are shown by small arrows, and the approximate size of each event is indicated by the number next to the arrow. The size of these stranding events along with their approximate geographical location names can be used to locate their positions on the images of Fig. 1.

Statistical analysis

Any statistical approach used to test for a relationship among the data shown on Figs 1 and 2 should be conducted with an awareness of two potential problems with the analysis. First, and as noted earlier, a regional trend exists in the USGS

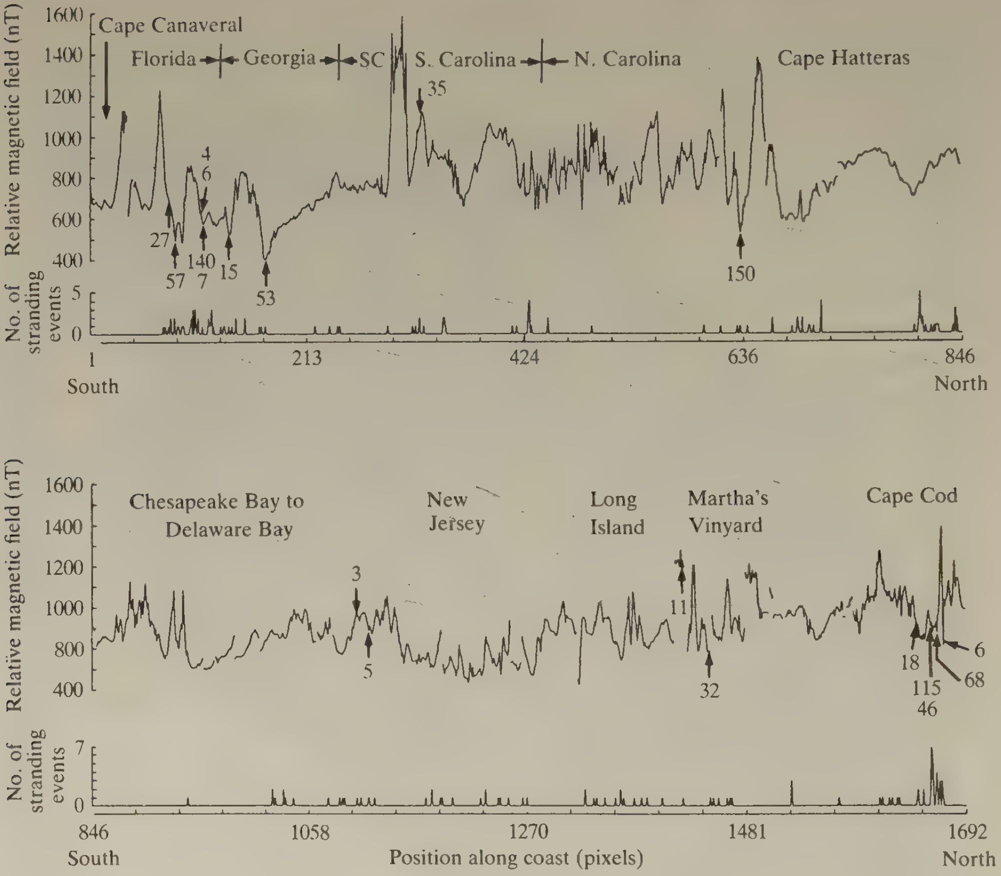


Fig. 2. Plot of the relative magnetic field in sequential segments along the coast from Cape Canaveral, Florida, through Cape Cod, Massachusetts, with a histogram showing the number of separate stranding events in each coast pixel. The data are shown in two halves, the upper and lower of which correspond approximately to the coastlines shown in Fig. 1A and B, respectively. Relative values for the magnetic data after subtraction of the IGRF are given in nannoTesla (nT) as described in the text, and the total variation shown is about 2 % of the total field strength before removal of the IGRF. Gaps in the magnetic curve show the boundaries between major adjacent coastal segments where the coastline has wandered out of the magnetic survey area or jumped to and from islands. (33 of the 40 coastal segments are large enough to be seen on this diagram, including all of those with stranding events. The other seven segments are only one or two pixels in length and not easily distinguished at this scale.) The average coastline length per pixel is 2·8 km. The location and size of mass stranding events are also indicated by the small arrows with the number of individuals in the stranded group. The location of southern state boundaries and other geographical reference points are shown along the top margin of each plot to aid in the location of each event on the images of Fig. 1.

aeromagnetic data as a result of incomplete removal of the IGRF. For this reason, any comparison of stranding locations with coastal field values should be restricted to those sub-regions without such obvious trends, or be made using only the relative field changes in the local coastal neighbourhood around each stranding site.

Similarly, care must be taken to compare each stranding event with its appropriate coastal segment. In all analyses conducted here, only those coastal segments which contain strandings of the cetacean group under consideration have been used as the basis for comparison.

The second, more subtle problem with this analysis arises from the gridded nature of the aeromagnetic data set. Although the north-south interval is a uniform 0·036° in latitude (or 4 km), the longitude width decreases as the cosine of the latitude. Southerly coastal pixels therefore represent a greater area than those in the North, and for this reason statistical tests should not be based directly on the distribution of magnetic field values at each coastal pixel. We avoided this problem by using the relative distance up or down the coastline from each stranding event as the basic measure for comparison.

At this point there are several statistical approaches which one might use to test for a relationship between stranding sites and the geomagnetic field. Perhaps the simplest (and most flawed) would be to ask whether the average field value at the strandings is significantly different from that of the coastal segment in question. Strandings near the bottom of local geomagnetic 'valleys' would produce a mean less than the coastal average, and the opposite for strandings near magnetic highs. Unfortunately, we have found that this general approach is easily biased by the presence of residual trends in the IGRF, and even by restricting the analysis to small segments of the coastline it is difficult to be confident of the results.

A better statistical approach is to examine the local coastal neighbourhood around each stranding event. A line of magnetic minima ('valley') where it intersects the coastline is at a position where the total field should increase away from the axis as followed from it up and down the coastline. The null hypothesis of no magnetic relationship to strandings implies that, on the average, the magnetic field along the coast should neither be higher nor lower than the magnetic field at the stranding sites. Therefore, the difference between the field value at a stranding and those from that of neighbouring coastline should on average be zero. Systematic departures from zero could either be due to strandings at extrema or adjacent to sharp magnetic highs or lows. Because this approach only compares the local field differences around a stranding event, the absolute field intensity is subtracted out and the problem of the regional bias in the IGRF discussed earlier is avoided. We have found that a suitable measure to test for stranding differences is to determine how close the field value at a stranding site is to the minimum and maximum values in its local vicinity. Let

$$x_{i,r} = \left(\frac{B_{i,\max} + B_{i,\min}}{2}\right) - B_{ith}\ \text{stranding}, \qquad (1)$$

where $B_{i,\max}$ and $B_{i,\min}$ are respectively the minimum and maximum field values within a distance of 'r' km from the i^{th} stranding site, and B_{ith} stranding is the field value at the i^{th} stranding. A suitable test of the null hypothesis is therefore to decide whether the average value of this group of magnetic field deviation parameters is distinct from zero; a significantly positive mean implies that strandings tend to happen close to local minima, and a negative mean implies that they strand near a local magnetic high. If $\bar{x}_r$ is the average of these values from equation 1 at a radius, r, based on i = N stranding events with variance, s^2, then the statistic

$$t = \frac{\bar{x}_r \sqrt{N}}{s} \tag{2}$$

will have the Student's *t*-distribution with (N−1) degrees of freedom (Sokal & Rohlf, 1981). Large magnitudes of t imply rejection of the null hypothesis, with the sign of t indicating strandings near either magnetically low or high places, respectively.

We conducted this analysis as a function of increasing radius (r) around the stranding sites in 5-km increments up to a maximum of 100 km (100 km is roughly the maximum distance a migrating whale could travel in 1 day). This procedure allows an estimate of the scale of magnetic features which might be influencing the choice of the cetacean's stranding sites. For each radius, only those strandings which were at least a distance r from the boundaries of its coastal segment were included. This constraint was imposed because the field is not continuous between adjacent coastal segments, and it is necessary to restrict this analysis to the particular stretch of coastline where the stranding happened. It is also improper to include a stranding event on a short coastal segment (or near an edge) if the current radius exceeds the continuous coastline on either side of it. In this analysis, therefore, the number of strandings included will monotonically decrease as the radius increases and strandings near the edges of coastal segments drop out. This is not a great problem, however, as the Student's *t*-statistic given in equation 2 allows for such variation in sample size.

The statistical approach outlined above lends itself to a direct check of significance through Monte-Carlo simulations, which, in addition, also provide a check of whether or not the Student's *t*-tests are applicable to the distributions at hand. A disagreement between the *t*-tests and the Monte-Carlo results would imply that the population of potential $x_{i,r}$ values drawn from the neighbourhoods around each stranding event is significantly non-normal. This might happen, for example, if there were a few large positive anomalies superimposed upon an otherwise randomly fluctuating background. As will be discussed later, this particular situation is common with geomagnetic data as a result of susceptibility anomalies. Note that significant deviations in mean field value (either high or low) from these tests imply that the cetaceans were following some cue related to the geomagnetic field. For this, two-tailed tests are clearly appropriate because we are interested in either high or low departures. Using two-tailed rather than one-tailed tests is also the conservative approach as it minimizes the risk of erroneously rejecting the null hypothesis (type I error).

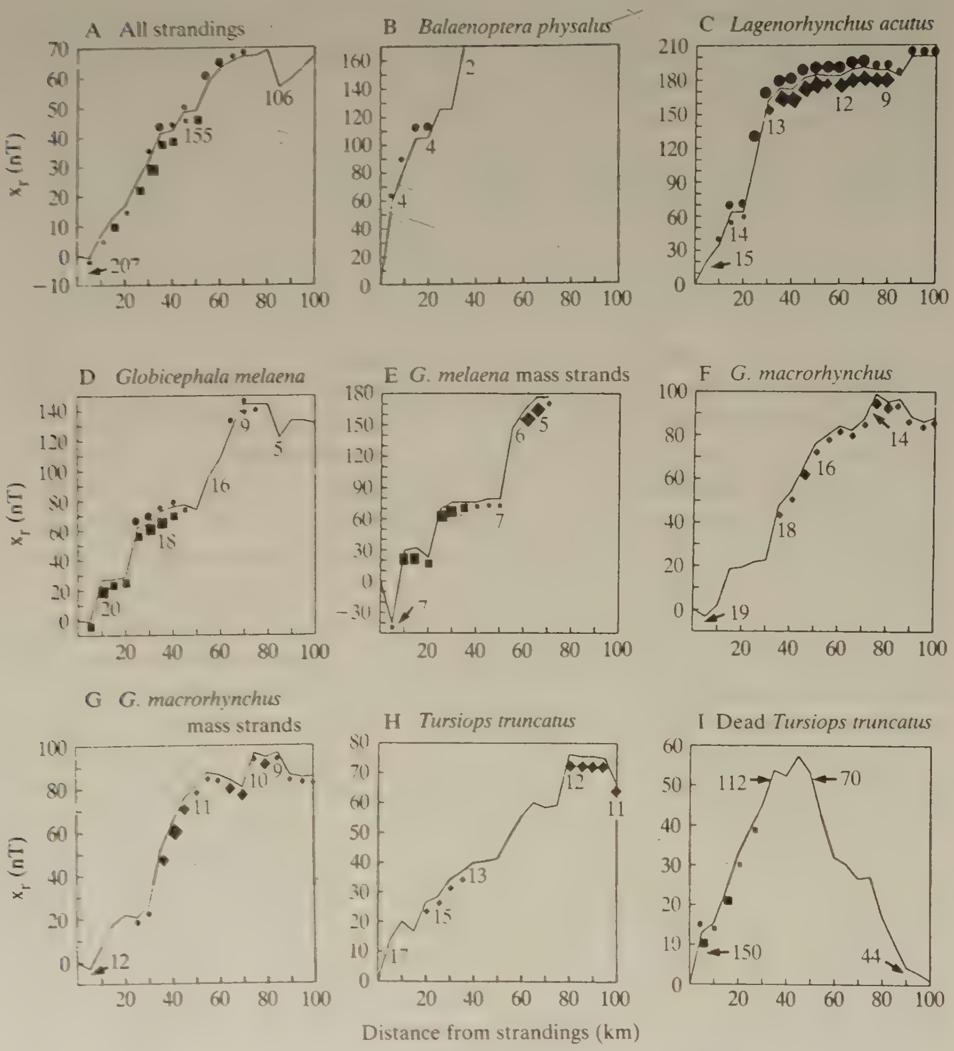
The Monte-Carlo method as we apply it to this problem involves first programming the computer to make a batch of 'random' whale positions equal in number to that present in each group of live strandings. We then calculate the set of $x_{i,r}$ values for this group using equation 1 in the same fashion as was done for the real batch. The mean value of this simulation for each radius is compared with that found for the real group and a record is kept concerning which is the largest or smallest. We then repeat this procedure 1000 or more times, and count the number of simulations with mean values greater than and less than that of the real group at each radius. This gives a direct measure of the significance of the real stranding set compared to random chance (e.g. if, at any particular radius, 5 Monte-Carlo simulations out of 1000 yield mean values less than that of the real cetacean group, one would reject the null hypothesis of no geomagnetic influence at the $P < 0{\cdot}005$ level on a one-tailed test, or at the $P < 0{\cdot}01$ level on the two-tailed tests used here).

From the discussion of Mead (1979) it is clear that there are regional biases in the reporting of cetacean stranding events in the Smithsonian database. These biases and the regional bias in the IGRF must be considered in the actual process of selecting random positions to match the strandings in the Monte-Carlo simulations. It is therefore very important that each random sighting 'observation' be created in such a fashion so as to be within a reasonable distance of its corresponding stranding event from the Smithsonian data set. For this purpose we defined an interval along the coast around each real stranding event within which one random stranding position was chosen per simulation. Points within this interval could not be more than 100 km from the real stranding site because we felt that this was a reasonable distance for a whale to travel in 1 day (swimming at about $4\,\mathrm{km\,h^{-1}}$), and was small enough to prevent the observing and IGRF biases from becoming serious. In addition, points within this interval could not be closer to either edge of coastal segment than was the real event. This constraint was necessary to prevent the Monte-Carlo whales from being thrown out of the analysis at a radius less than that of the whale it was supposed to simulate. Finally, a random whale was thrown out of the analysis at radii above the maximum for the real event in order to match the number of random whales with real whales at each radius.

The Monte-Carlo simulations also permit another type of check on the distribution of stranding sites relative to the magnetic field. It is conceivable that cetaceans might choose to strand at coastal locations with abnormal variations in the field (e.g. places where not only the $\bar{x}$ values are distinct relative to the geomagnetic field, but that the variance, s^2, may also be significantly non-random). This situation could arise, for example, if at different times during the year the preference within a species shifts from magnetic lows to highs, or if they are responding to field gradients in some fashion. Therefore in each of our 1000 Monte-Carlo simulations, we also calculated the s-values and compared them with those observed in the actual stranding data set.

RESULTS

Results from the analyses described above are shown in Fig. 3 for each species or subgroup within the stranding data set. In these diagrams, the average value of the magnetic field deviation parameter ($\bar{x}_r$ from equation 1) is plotted at intervals of 5 km from the stranding sites out to a distance of 100 km. Results from the Monte-Carlo simulations are also shown at each radius value by a series of circle, square and diamond symbols in three sizes (small, medium and large; small symbols imply significance at $P < 0{\cdot}05$, medium at $P < 0{\cdot}01$, and large at the $P < 0{\cdot}001$ level on two-


A All strandings

B *Balaenoptera physalus*

C *Lagenorhynchus acutus*

D *Globicephala melaena*

E *G. melaena* mass strands

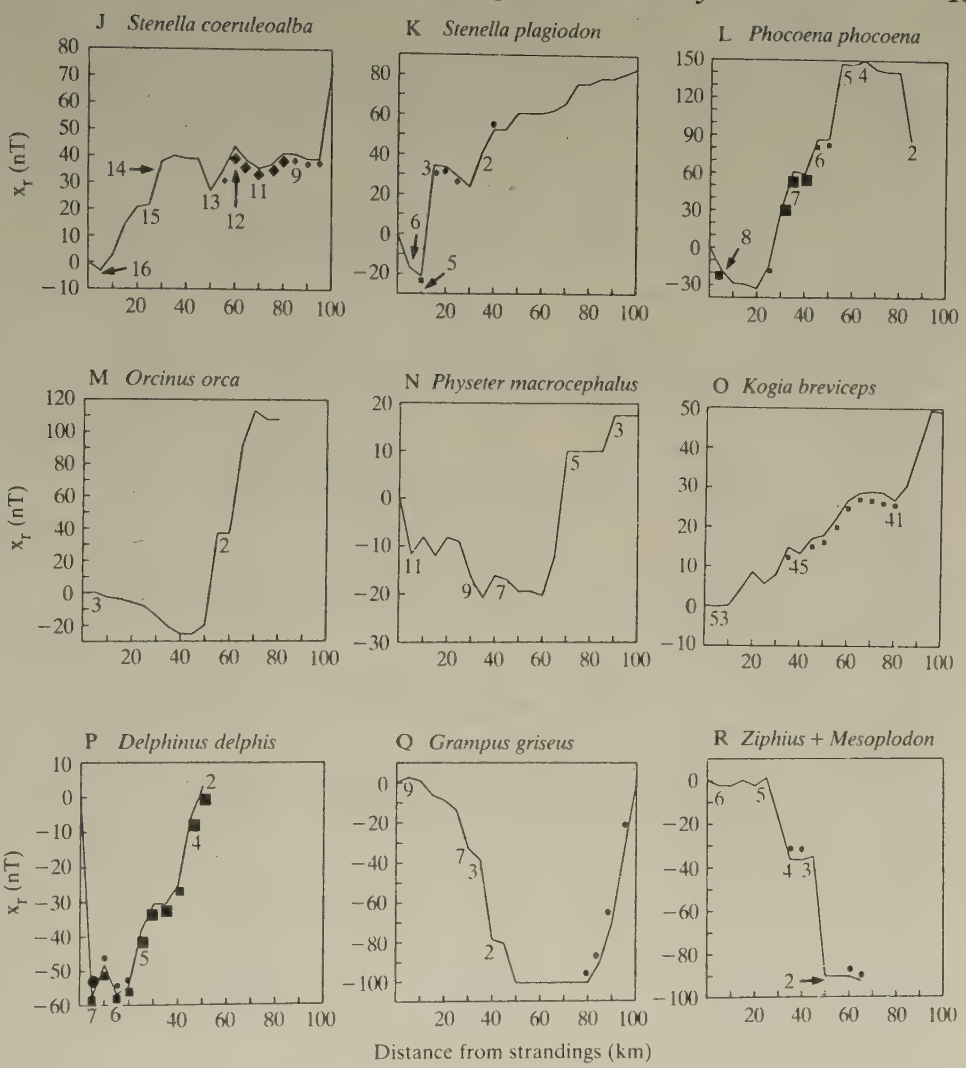
F *G. macrorhynchus*

G *G. macrorhynchus* mass strands

H *Tursiops truncatus*

I Dead *Tursiops truncatus*

Fig. 3. Average magnetic field deviation parameters (in nT) (from equation 1) as a function of distance from stranding events. Values of this parameter were calculated in 5-km increments up to 100 km for each of the species groups indicated. Positive values imply that the strandings preferentially happen near local magnetic minima, while negative values imply strandings near local magnetic highs. These figures therefore give a clue as to the shape of the average magnetic 'valley' or 'hill' around which the strandings occur. At each radius value, significant deviations of either the mean or variance of the deviation parameters (measured through the Monte-Carlo simulations) are indicated by the size of the circle, square or diamond symbols as follows: small implies $P<0.05$, medium implies $P<0.01$, and large implies $P<0.001$ on two-tailed tests. The circles show results from the comparison of mean values, while diamond and squares show results from the variance comparison with diamonds and squares respectively indicating low and high. Numbers written below the curves give the number of stranding events left in the analysis at that radius.



tailed tests). Circles indicate departures of the mean value of $\bar{x}_r$ with its sign indicating whether it was towards high or low fields. Similarly, the diamond symbols indicate that the variance of the $x_{i,r}$ values was significantly low while the squares indicate abnormally high variance.

Table 1 lists typical results from these analyses for the 14 separate species in which we have three or more stranding events within the magnetic data area. For species which strand more rarely we have grouped them into the nearest taxonomic categories (e.g. all family Ziphiidae, the miscellaneous Delphinidae, and all Balaenopteridae). Two species (*Globicephala melaena* and *G. macrorhynchus*) account for most of the live mass stranding events which happen within the magnetic data area (8 and 11 respectively), and for these we have also run separate analyses giving unit weight to all events in which three or more individuals were stranded. In addition, we ran the analyses on the entire live stranding data set of 212 events and 158 records

Table 1. *Results of the neighbourhood analyses as shown on Fig. 3 at representative radii for various species and groups of cetaceans examined in this study*

SUB-ORDER	Family	Species and common name	Number of strandings survey area	Neighbourhood extremes						Monte-Carlo *P*	
				Radius (km)	Number with this radius	Average local field deviation (nT)	Standard deviation (s,nT)	*t* (n−1 d.f.)	*P*	Mean	Variance
		All species combined	212	35	168	41·4	114·4	4·69	<0·001***	0·006**	$0{\cdot}002_{\mathrm{II}}^{**}$
ODONTOCETI (toothed whales)	Delphinidae	*Globicephala melaena* (long-finned pilot whale) All	22	70	9	144·4	56·1	7·73	<0·001***	0·046*	$0{\cdot}016_{\mathrm{L}}^{*}$
		Only mass strandings	8	60	6	164·6	10·9	36·83	<0·001***	0·09	$<0{\cdot}001_{\mathrm{L}}^{***}$
		Globicephala macrorhynchus (short-finned pilot whale) All	19	75	14	99·0	116·9	3·17	<0·01**	0·57	$0{\cdot}008_{\mathrm{L}}^{**}$
		Only mass strandings	11	45	12	75·3	75·5	3·46	<0·01**	0·28	$0{\cdot}004_{\mathrm{L}}^{**}$
		Stenella coeruleoalba (striped dolphin)	17	60	12	43·6	37·3	4·05	<0·01**	0·63	$0{\cdot}01_{\mathrm{L}}^{**}$
		Stenella plagidon (spotted dolphin)	6	15	3	34·7	3·5	17·09	<0·01**	0·08	$0{\cdot}014_{\mathrm{L}}^{*}$
		Lagenorhynchus acutus (Atlantic white-sided dolphin)	16	30	13	161·9	29·2	20·02	<0·001***	<0·001***	$0{\cdot}002_{\mathrm{L}}^{**}$
		Tursiops truncatus (bottlenose dolphin)	17	80	12	76·3	73·9	3·57	<0·01**	0·35	$0{\cdot}005_{\mathrm{L}}^{**}$
		Dead *Tursiops truncatus*	158	5	150	12·9	58·7	2·70	<0·01**	0·012*	$0{\cdot}008_{\mathrm{II}}^{**}$
		Grampus griseus (Risso's dolphin)	9	30	7	−32·6	68·1	−1·27	>0·20	0·09	0·998
		Delphinnus delphis (common dolphin)	7	15	6	−56·8	127·3	−1·09	>0·20	0·012*	$0{\cdot}006_{\mathrm{II}}^{**}$
		Orcinus orca (killer whale)	3	55	2	36·8	3·2	16·3	<0·05*	0·66	$0{\cdot}11_{\mathrm{L}}$
		Miscellaneous Delphinidae	5	60	3	170·3	68·5	4·3	<0·05*	0·24	$0{\cdot}34_{\mathrm{L}}$

Table 1. *Continued*

SUB-ORDER	Family	Species and common name	Number of strandings survey area	Neighbourhood extremes							
				Radius (km)	Number with this radius	Average local field deviation (nT)	Standard deviation (s,nT)	t (n−1 d.f.)	P	Monte-Carlo P	
										Mean	Variance
ODONTOCETI (toothed whales)	Physeteridae	*Physeter macrocephalus* (sperm whale)	11	45	7	−16·9	70·4	−0·64	>0·50	0·15	$0{\cdot}68_{L}$
		Kogia breviceps (pigmy sperm whale)	53	50	45	18·1	149·6	0·83	>0·20	0·60	$0{\cdot}018^{*}_{H}$
		Kogia simus (dwarf sperm whale)	6	70	6	32·7	187·3	0·43	>0·50	0·78	$0{\cdot}36_{H}$
		Phocoenidae Phocoena phocoena (harbour porpoise)	8	35	7	61·1	160·0	1·01	>0·20	0·22	$<0{\cdot}001^{***}_{H}$
		All family Ziphidae	6	35	4	−36·1	70·0	−1·03	>0·20	0·046*	$0{\cdot}44_{H}$
MYSTICETI (baleen whales)	Balaen-opteridae	*Balaeneoptera physalus* (fin whale)	4	20	4	105·1	74·7	2·82	>0·05	0·006**	$0{\cdot}702_{H}$
		All Balaeneoptera	7	15	7	59·2	71·2	2·2	>0·05	0·014*	$0{\cdot}19_{H}$

In this table, the number of strandings in the survey area refers to those stranding events which were accurately located and occurred within the boundaries of the U.S.G.S. aeromagnetic data set. The radius value given in the table is the distance for which the local field deviation parameter of equation 1 in the text has been calculated, and for which the results are included in this table. As can be seen on Fig. 3, these values have been chosen as typical for those intervals where the departures from the null hypothesis are most pronounced. Also given in the table are the number of stranding events which remain in the analysis at that radius (these correspond to the small numbers on the diagrams of Fig. 3), the average value of the parameter (x) from equation 1, the standard deviation(s) around the mean value of this parameter, the value of Student's t-statistic and P-value for two-tailed tests, and the significance of both the mean and variance of the distribution as measured through Monte-Carlo simulations. For all of the probability levels, * indicates $P < 0{\cdot}05$, ** indicates $P < 0{\cdot}01$, and *** indicates $P < 0{\cdot}001$ on two-tailed tests. The subscripts L and H on the variance Monte-Carlo results indicate whether the actual stranding value was on the low or high side (respectively) in comparison to the 1000 or more Monte-Carlo simulations.

of dead *Tursiops truncatus* which were highly decomposed when found (decay types 4 and 5 from the Smithsonian listing).

The tendency for most cetaceans to strand near magnetically low spots is apparent in their combined results (Fig. 3A; Table 1). Significantly positive values of the magnetic field deviation parameters are achieved within a 15-km radius of the stranding sites (with the t-statistic), and this becomes and remains very highly significant ($P < 0{\cdot}001$) above 20 km. This result does not depend upon our use of the deviation parameter of equation 1, as we have obtained similar results using several other measures of where strandings occur relative to local magnetic field variations (including a weighted average of the field deviations up and down the coastline).

The Monte-Carlo simulations, however, present an interesting but somewhat more conservative picture as shown on Fig. 3A. Positive values of the mean deviation parameters are significant in the 30- to 70-km interval, with the highly significant ($P < 0{\cdot}01$) levels being reached three times. This difference between the Student's t-test and the Monte-Carlo simulations is probably due to the presence of more magnetic highs than lows along the coast as can be seen on Fig. 2 and was mentioned earlier. This asymmetry will tend to add a small positive slope to the diagrams in Fig. 3 which, in turn, will tend to bias the t-tests towards more significant results. For this reason we follow the conservative approach and base our conclusions on the Monte-Carlo results rather than solely on the t-tests.

In addition, the Monte-Carlo simulations reveal that the variance of the deviation parameters for the combined stranding group is abnormally high at radii ranging from 5 to 55 km ($P < 0{\cdot}05$ to $P < 0{\cdot}001$). It therefore seems that either the overall set is inhomogeneous (e.g. some small fraction of the cetaceans may be seeking the magnetic highs rather than the lows in which to strand), or that sections of coastline with unusually high magnetic variability tend to attract strandings. To explore further the source of this variance, we subdivided the total stranding data set into the various species and ran the same Monte-Carlo analyses on them.

Highly significant tendencies ($P < 0{\cdot}01$ or $P < 0{\cdot}001$) for strandings to happen at magnetic minima were observed in *Lagenorhynchus* (Fig. 3C), *Balaenoptera* (Fig. 3B) and *Globicephala* (Fig. 3D) despite the smaller sample size when compared to the whole group, and significant ($P < 0{\cdot}05$) tendencies in the same direction were observed in *Tursiops* (Fig. 3I) and *Stenella* (Fig. 3K).

This tendency for cetaceans to strand at magnetically low spots is clearly seen in Fig. 4A,B. In both of these diagrams the profiles of the magnetic field around the stranding events have been superimposed on top of each other with both the relative coastal distance and magnetic fields set to the point (0, 0) in the centre as indicated by the thick horizontal and vertical lines on each diagram. These graphs resemble 'spiders' with long thin legs all radiating out from a central point. If all strandings for a species were to happen exclusively at local magnetic minima, all of the spiders' 'legs' would point forward (up) into the top quadrants on both sides of its centre. Similarly, stranding points at magnetic highs will send the 'legs' downwards into the bottom quadrants, and a magnetically random set of strandings will yield a pattern of legs radiating out in all directions. Both of the spider plots shown in Fig. 4

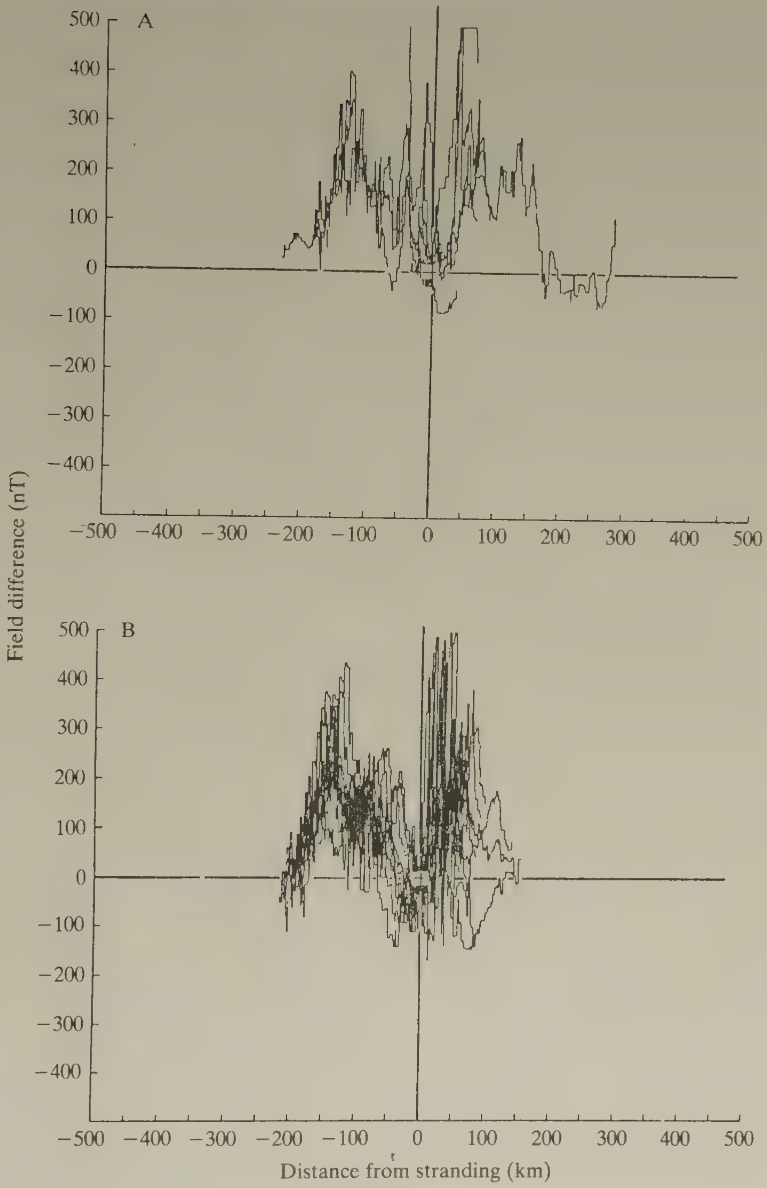


Fig. 4. Spider diagrams of the magnetic field around stranding positions. For both species shown, all of the stranding events have been stacked so that their geographical and magnetic positions coincide at the centre of the diagram. Away from this central point, the magnetic field changes are plotted as a function of total coastline distance within each pixel (north to the right), and each line on the plot is terminated at the end of its respective coastal segment. These diagrams therefore show all of the data which are used in making the diagrams of Fig. 3. The lines (or 'spider legs') will all point upwards away from the centre if strandings are happening at local magnetic minima, and will point downwards if they are at local maxima. Thus, the null hypothesis of no relationship of strandings to the geomagnetic field predicts that there should be roughly equal numbers of 'legs' in each of the four quadrants around the centre of the diagram, which is clearly not the case. (A) *Balaenoptera physalus* (fin whale); (B) *Lagenorhynchus acutus* (Atlantic white-sided dolphin).

are from species (*Balaenoptera physalus* and *Lagenorhynchus acutus*) which give strong results for the analyses of Table 1 and Fig. 3; the average tendency for the arms to point upwards is clear.

On the other hand, three of the groups including *Delphinus* (Fig. 3P), *Grampus* (Fig. 3Q), and the family Ziphiidae (Fig. 3R) display the opposite tendency ($P < 0{\cdot}05$) of stranding at magnetic highs, with *Delphinus* reaching a very highly significant deviation ($P < 0{\cdot}001$) at only 5 km. These 22 stranding events, however, are only 10 % of the total number of records and by themselves would probably not be enough to cause the large variance noted above in the total stranding group.

Several of the species groups also have surprisingly high variance measurements (indicated by the square symbols on Fig. 3) irrespective of whether or not they have significant tendencies to strand at either minima or maxima. These include *G. melaena* (Fig. 3D,E), the dead *Tursiops* (Fig. 3I), *Phocoena* (Fig. 3L), *Kogia breviceps* (Fig. 3O) and *Delphinus* (Fig. 3P). These high variances are associated with tendencies to strand both at maxima (e.g. *Delphinus*, Fig. 3P) and minima (e.g. *G. melaena*, Fig. 3D). As one might expect, several groups which have this high variance show no significant tendency to strand at minima or maxima, and could be composed of inhomogeneous groups doing both (e.g. *G. melaena, Phocoena phocoena, Kogia breviceps*) as discussed below.

None of the analyses presented so far give clues as to whether or not any of the cetaceans were following continuous paths of local magnetic minima when they intercepted the coastline. The most continuous such path in our data set, however, is the prominent part of the East-coast magnetic anomaly which runs ashore in the middle of the Georgia coast (seen as a deep blue streak on Fig. 1A). Two of the mass stranding events happen where branches of this East-coast magnetic minimum run ashore. These are the only mass stranding events in Georgia and can be seen in the top diagram of Fig. 2 labelled by the arrows indicating groups of 15 and 53. Both are precisely at the minima of the valleys. Visually at least, our data are compatible with the hypotheses that some of the cetaceans were following these magnetic minima prior to beaching themselves. Although this observation is suggestive, it should be checked with similar data from the prominent marine magnetic lineations over true oceanic crust.

Klinowska (1983) reports using the locations of beached cetacean carcasses as a control for comparison with live stranding events. A major assumption in this approach is that the animals died at sea and were then washed ashore; from the Smithsonian listings used in our study it is often difficult to distinguish this from true live stranding events which were not discovered until long after the animals died and decayed (Mead, 1979). For this reason one might expect some similarity in the magnetic parameters of both live and dead strandings. We ran these analyses on 158 positions for badly decomposed (types 4 and 5) *Tursiops truncatus* given in the Smithsonian listing because this is predominantly a coastal animal (Mead, 1979). We again found a weak but significant correlation with low magnetic fields and a high variance (Table 1; Fig. 3I, radius 5 km), suggesting that this may indeed be the case.

DISCUSSION

It seems clear from the analyses presented above that there is a statistically robust relationship between cetacean live stranding positions and the residual geomagnetic field along the U.S. Atlantic continental margin. Significant tendencies to strand at locations with low magnetic intensity were found in species from both suborders of Cetacea. The question then is whether or not cetaceans possess a geomagnetic sensory system capable of guiding their way, or whether other environmental parameters such as bathymetry or currents could be responsible for the observed effect.

Klinowska (1983 and written communication) found no relationship with the geomagnetic field and the locations of dead whales which washed ashore, indicating that there is no apparent relationship between oceanic water currents, tides and geomagnetic anomalies. (Unlike the American stranding records, it is apparently possible to separate true live stranding events from dead carcasses washing ashore in the British records.) Oceanic currents also tend to intersect the coastline on a much larger scale (thousands of km) than the typical variations in the geomagnetic field (10–100 km scale). Live strandings also seem to happen with roughly equal probability on both rocky and sandy beaches (Geraci & St. Aubin, 1979).

A bathymetric effect is perhaps a more viable alternative hypothesis to account for the observed relationships with the magnetic field. In areas of high latitudes with steep magnetic inclination, a submarine canyon or valley which has cut through geological strata of uniform susceptibility will locally weaken the geomagnetic field at the ocean surface. If cetaceans were attempting to follow such bathymetric features (with echolocation, for example) when they beached themselves, a correlation between stranding location and geomagnetic intensity might result. Of course, this hypothesis predicts the existence of bathymetric relief along the Atlantic continental shelf which mirrors the magnetic variations and requires that the basement has enough magnetic susceptibility to produce measurable anomalies at the surface. To test this hypothesis we examined the large-scale (1:1 000 000) map series compiled by Belding & Holland (1970) and published by the American Association for Petroleum Geologists (AAPG). Most of the offshore topography along the Atlantic continental margin is basically flat, due to the bevelling effect of numerous glaciogenic sea-level transgressions and regressions during the Pleistocene. In general, the topography along this coast is subdued and characterized by barrier islands, with average regional slopes on the shelf of less than 1° (McGregor, 1984). None of the major magnetic lineaments seen in Fig. 1 has any visible relationship with nearshore bathymetry, and even the well-developed submarine canyons off the New Jersey and New York coasts (e.g. Hudson & Baltimore Canyons) fail to show up on the magnetic map of Fig. 1.

The apparent lack of correlation between the bathymetric and aeromagnetic data for the Atlantic margin is a fairly straightforward result of its geological history. The North American plate broke away from the supercontinent of Pangea roughly 160 million years ago during a rifting event which led to the formation of the Atlantic Ocean. As these plates moved apart, the highly magnetic volcanic rocks associated with the rifting event were gradually buried under a blanket of weakly magnetized sediments which in some areas reach a thickness of 14 km (McGregor, 1984). Thus, with the exception of more recent volcanism associated with seamounts, the magnetic characteristics of the continental shelf are still dominated by deeply buried volcanic rocks. For example, the large magnetic high which marks the transition from the continental shelf to the slope (this is called the 'Blake Spur' magnetic anomaly and can be seen as a NE–SW trending yellow streak on Fig. 1A) is related to the rift-related faulting and volcanism which formed during the break-up event, and can be seen in the seismic profiles of Alsop & Talwani (1984). In contrast, the overlying sediments generally have such a low magnetic susceptibility that even a large valley near the surface will yield little, if any, aeromagnetic expression. Therefore, it seems unlikely that the geomagnetic stranding correlations noted earlier could be an artifact of bathymetry in this region.

The simplest remaining hypothesis is that cetaceans possess a highly developed sensitivity to the geomagnetic field which enables them to use local variations in it for guidance, and that this is reflected in their stranding locations. In turn, this implies the presence of specialized receptors capable of transducing weak geomagnetic stimuli to the nervous system. Note that many of the stranding positions seen on Fig. 2 suggest that total intensity variations of less than 50 nT (0·1 % of the total field) are enough to influence stranding location. (Similar K-index correlations imply the same order of sensitivity in birds, a topic which is discussed by Gould, 1982; Kirschvink, 1982, 1983 and Kirschvink & Walker, 1985.)

Klinowska (1983) has also suggested that live cetacean strandings tend to happen where local minima ('valleys') in the geomagnetic total intensity field cross the British coastline, and that they actively avoid entering areas of locally higher intensity. (Note this does not address the question of why they strand.) This effect is similar to the observation of Walcott (1978) that pigeons released at magnetic anomalies are confused. Further analysis of Walcott's data (Gould, 1980, 1982; Kirschvink, 1982) also shows a tendency for the birds to avoid local magnetic highs during the initial phase of flight, a strategy which probably aids in their initial assessment of their position relative to the home loft. The weak strength of the magnetic variations which produce these effects and their occurrence on sunny days (when sun-compass orientation is possible) implies that the response is more than a simple compass one. Rather, it probably depends on an ability to sense small fluctuations or changes in the total intensity field (Kirschvink & Gould, 1981; Kirschvink, 1982).

These variations are so small that the overall effect is probably not the result of a simple directional compass, and the extreme sensitivity is difficult to achieve with a magnetic sensory system based on electrical induction (Jungerman & Rosenblum, 1980; Rosenblum, Jungerman & Longfellow, 1985). Ferromagnetic material (probably magnetite) has been reported in the head region of cetaceans by Zoeger, Dunn & Fuller (1981) and more recently by Bauer *et al.* (1985), but the authors found so much magnetic material in the tissues that they could not focus on any specific site as the focus of a possible sensory organ as has been done for yellowfin tuna, *Thunnus albacares* (Walker *et al.* 1984). Large numbers of magnetite-based magnetoreceptors could in theory yield the required geomagnetic sensitivities if arranged in a signal-averaging network (Kirschvink, 1979; Kirschvink & Gould, 1981; Yorke, 1981; Kirschvink & Walker, 1985). The recent extraction of chains of magnetite crystals from the dermethmoid tissue of salmon (Kirschvink *et al.* 1985) also suggests that the general vertebrate magnetoreceptor may be something like a modified hair-cell mechanoreceptor; it certainly seems worth conducting similar investigations in cetaceans.

Why is there a general tendency for the strandings to happen at geomagnetic minima rather than maxima? A migrating animal on the oceans would be equally able to follow the magnetic highs, lows, or perhaps the maximum gradients during a long journey, as all of these would help maintain track of relative longitude using the marine magnetic lineations. However, the simplest approach is to follow the local minima, because both the highs and gradients are more prone to a positive susceptibility bias from seamounts and oceanic fracture zones. In addition, many migratory animals regularly cross the boundary between the continental shelf and the oceanic crust in their travels, and a strategy of avoiding high fields and gradients could be used over both continental and oceanic terrains. For this reason, marine magnetic lineations are reasonable features in the magnetosphere for animals to follow, and their relationship with migration routes (if any) warrants further investigation, particularly at sea. Despite this, cetaceans might have other uses for geomagnetic cues even while they are not migrating. Some seamounts (or Guyots), for example, are characterized by higher levels of productivity than the surrounding waters, and cetaceans may exploit this. Seamounts generally produce a large, symmetrical magnetic 'hill' superimposed on the undulating magnetic topography of the oceans, one of which is the only bright yellow spot on the eastern margin Fig. 1B.

A few of the mass stranding events do happen near clear magnetic maxima, an example of which is the group of 35 short-finned pilot whales (*G. macrorhynchus*) which went ashore on Kiawah Island near Charleston, South Carolina, on 2 November 1973 (visible on Figs 1A and 2 as the only mass-stranding event in South Carolina). Coupled with the apparent tendency for three of the groups in the analysis (*Delphinus*, Fig. 3P; *Grampus*, Fig. 3Q; and Family Ziphidae, Fig. 3R) to strand near magnetic maxima, this would suggest that the cetacean's choice of whether to follow magnetic lows or highs may depend upon a variety of unknown behavioural conditions. The stranding data set may in general be biased towards the lows, as strandings are thought to occur more often in animals which are migrating or otherwise outside their familiar territory (Mead, 1979). However, a smaller fraction of strandings may occur at other times. This line of reasoning predicts that a similar analysis of the position of cetaceans at sea may find seasonal and/or regional shifts from one magnetic state to another depending upon behaviour (e.g. lows may be sought during migration, and the highs might be used during feeding or while trying to remain in one place). A situation of this sort could lead to the high variance values found in several of the species groups mentioned earlier. This is clearly the case of the *G. melaena* mass strandings; as seen in Fig. 3E the variance abruptly changes from high to low (square to diamond symbols) when the Kiawah Island event is thrown out of the neighbourhood analysis after the 55 km radius.

Results from this study lead to an interesting and testable prediction concerning the abundance of whale bone fossils in tertiary nearshore sediments along the Atlantic continental margin. Locations where such long, continuous magnetic minima cross the coastline (like those in Georgia, Fig. 1A) should generate a substantially higher flux of whale bones to surrounding sediments, and there should be measurable variations in their local abundance associated with the magnetic topography. Similarly, when the Earth's magnetic field reverses itself many of the local minima will turn into local maxima (and *vice versa*), and the stranding flux should shift to other points along the coastline. This predicts that in places where magnetic lows currently cross the coastline, whale bone fossils should be more numerous in sediments deposited during normal polarity intervals than during times of reversed polarity. In a continuous section spanning long intervals of time, it should be possible to predict the magnetic polarity pattern based on the abundance of whale fossils. Numerous sedimentary deposits are known along the Atlantic coastline where this prediction could be tested (e.g. Ray, 1984).

In summary, the cetacean live-stranding records from the U.S. Atlantic continental margin strongly support the hypothesis that they are using some features of the geomagnetic field while finding their way. This study and that of Klinowska (1983) reach similar conclusions, and both predict that cetaceans located and/or tracked at sea should show similar relationships with respect to the marine magnetic lineations. If this proves to be true, it would have major implications for commercial fisheries which exploit magnetically-sensitive fish like tuna (Walker, 1984) and salmon (Quinn, Merrill & Brannon, 1982), as well as perhaps lead to better techniques for resource estimation and management. We are at present testing this hypothesis with sighting records of 25 000 marine animals from the Cetacean and Turtle Assessment Program (U.S. Bureau of Land Management) along the Atlantic Margin.

We thank Dr James Mead of the Smithsonian Marine Mammal Program for providing us with the stranding data and Dr D. Clark of the National Geophysical Data Center for the USGS Aeromagnetic data. L. Dizon and A. Kobayashi-Kirschvink patiently sorted through and checked numerous stranding records, and Ed Danielson (of JPL) and Jerry Kristian (Caltech) aided the preparation of the colour images of the magnetic field. M. M. Walker gave critical advice on the manuscript. Contribution No. 4123 from the Division of Geological and Planetary Sciences, California Institute of Technology. Supported through NSF grants BNS83-00301 and PYI-8351370 to JLK.

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LUTJANIDAE

by Steven H. Kramer

Valid name	*Aprion virescens* Cuvier and Valenciennes 1830 (Fig. 60)
Synonymy	*Mesoprion microchir* Bleeker 1853 *Lutjanus macrochir* Bleeker 1863 *Sparopsis latifrons* Kner 1868 *Sparopsis elongatus* Kner 1868 *Chatopterus microchir* Bleeker 1869 *Aprion* (*Aprion*) *virescens* Bleeker (1872) 1873, revision *Lutjanus*, 1876-77 (from Weber and De Beaufort 1936)
Common and vernacular names	Blue-green snapper; jobfish; uku

Distribution:

Caught only at Nihoa, Brooks Banks, St. Rogatien, and Midway in the NWHI. Maximum depth recorded for this species was 58 m.

Frequently inhabits midwater near reefs and drop-offs in depths of 6-28 m and never takes shelter in the coral (Talbot 1960). Feeds in the water column from surface to the bottom (Ommanney 1953; Wheeler 1953).

Distinguishing characteristics

D. X, 11; A. III, 8; P1. 17; LLps. 48-50; Gr. 7+14-15 (Masuda et al. 1975). Body elongate, more cylindrical than slender with large scales. Head with prominent groove on either side of snout in front of eyes; eyes relatively small, high on head. Pectoral fins short, rounded; single dorsal fin without a notch; dorsal and anal fins scaleless. Caudal fin deeply forked. Attains a length of 1 m.

Mouth oblique; lower jaw slightly projected; both jaws with two strong anterior canines. Smaller canines located laterally and between the strong canines. Villiform bands on both jaws with outer series enlarged. Vomerine teeth form a curved patch, palatines an elongated ovate patch.

In life, light gray-blue or gray-green laterally, with blue reflections dorsally, becoming much lighter ventrally. Violet blotches occur at base of soft membrane of spinous dorsal fin. Pectoral and ventral fins are yellowish (Fischer and Whitehead 1974).

Life history

Little is known about the life history of uku in Hawaiian waters. On the East African coast, fully ripe females were found in all months except June and August, suggesting a breeding season in the warmer months (Ommanney 1953; Wheeler 1953; Williams 1956; Talbot 1960). Partially ripe females were recorded in all months, but the species may actually have an irregular extended breeding season (Talbot 1960). Williams (1956) reported sexual maturity occurring at about 60-75 cm for both sexes, but Talbot (1960) found females fully ripe at 46.5 cm SL and males at 50.0 cm SL. This species can be solitary or occur in loose, well-spaced aggregation of two to five fish. In the main islands, they appear to congregate during their spawning period which generally occurs in June (see footnote 6).

The length-weight relationships are probably the same for both sexes; however, no definitive equation expressing the relationship between length and weight is available (Williams 1956).

Uku is a high-level predator in the food chain, preying on fish, crustaceans, cephalopods, and zooplankton. It also feeds on larger fish such as scombrids (Reintjes and King 1953).

Food items found in *A. virescens* stomachs from East Africa consisted of fish (49%), plankton (17%), cephalopods (14%), nonplanktonic crustaceans (12%), and others (8%) (Talbot 1960). Identifiable food items included *Siganus oramin*, *Caesio caerulaureus*, *Sphyraena* sp., and *Sardinella* sp., members of the Families Callyodontidae, Ostraciontidae, and Bothidae; squids; portunids crabs, penaeid shrimps, and *Squilla* sp.; and planktonic organisms such as fish eggs, larval and postlarval fishes, stomatopod larvae, salps, and zoeae larvae (Ommanney 1953; Wheeler 1953; Williams 1956; Talbot 1960).

Uku has been reported to be ciguatoxic at Enewetak and Bikini Atolls (Randall 1980). In Hawaii, this species has been implicated in three ciguatera attacks since 1900 (see footnote 11).

Gear and catch

Uku is caught primarily by handline and set lines, rarely by rod and reel and trolling gear. The uku is the only Hawaiian lutjanid regularly caught at or near the surface with lures. Considered an excellent food and game fish, the annual landings in 1961-79 varied between 19,192 and 40,730 kg, and averaged 28,909 kg, making it second in importance to the opakapaka among the snappers in the local fishery. Landings are seasonal the bulk of the catch is made from June to December (see footnote 6).

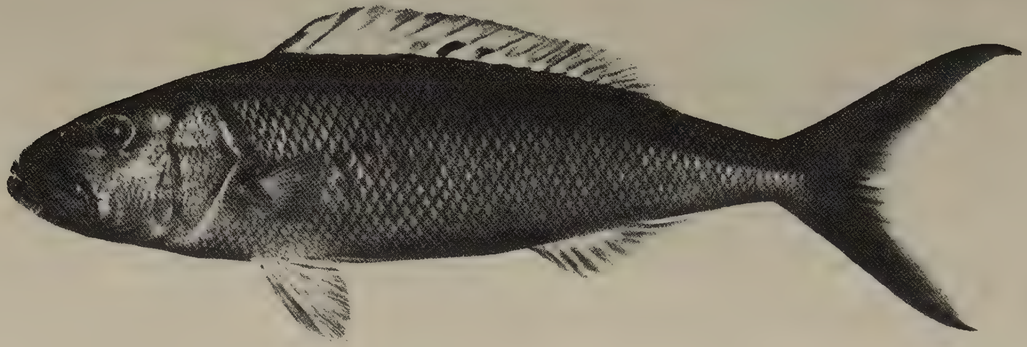

Figure 60.—*Aprion virescens*.

OCTOPODIDAE

by Steven H. Kramer

Valid name	*Octopus cyanea* Gray 1849 (Fig. 46)
Synonymy	*Octopus marmoratus* Hoyle 1885 *Octopus horsti* Joubin 1898 *Polypus marmoratus* Hoyle 1905 *Polypus horsti* Hoyle 1907 *Polypus cyanea* Massey 1916 *Polypus fontanianus* (in error) Robson 1920 *Octopus glaber* Wilker 1920 (from Robson 1929)
Common and vernacular names	Octopus; day octopus; day squid; tako; hee

Distribution

Captured in traps in the NWHI from Necker to Kure Atoll at depths from 18 to 91 m. It also inhabits rocky substrates and reef flats shoreward of the NMFS survey area.

Distinguishing characteristics

Body shape variable but usually pyriform, head rather small, narrow, and rounded, sometimes separated from the body by a slight constriction, eyes prominent. Arms subequal (rarely <30 mm difference in length) unless an appendage is missing or regenerated.

A small hectocotylus used to transfer spermatophore located on the distal end of the third right arm of males. Suckers on sexually mature males enlarged at the level of the web on each arm. Funnel organ small, conical. Skeletal structures consist of cephalic cartilages and dorsal stylets. Beak has insertion plate on which is fixed the upper and lower horny jaws. Shape differs little within the genus. Carnivorous type radula. Ink sac on ventral face of liver; gills consist of a number of filaments suspended from opposite sides of a central axis forming two closely opposed series; skin texture usually smooth but can assume a rough matted appearance in life and during preservation. Few large dorsal tubercles can be longitudinally extended. Supraocular cirrhus usually present, sometimes accompanied by subordinate tubercles. Ocellus below eye and between base of third and fourth arms.

Coloration usually cryptic but varies according to animal's physiological state and habitat; most often a warm ochreous red suffused and blotched with purple. Irregular dark dashes often present between suckers on ventral surface of the arms (Robson 1929).

Life history

Hee appears to spawn throughout the year (Van Heukelem 1973). Males copulate by inserting the hectocotylus into the female's oviduct. At the hectocotylus, spermatophores break open and expel sperm. The oviduct contracts and sperm is carried up to lodge in the spermathecae of the oviducal glands. Females do not have to be sexually mature for copulation to take place (Wells and Wells 1970).

Females reach sexual maturity 10-13 months after settling. Strings of 600-1,200 eggs measuring 4-10 cm long are laid in caves or holes. Brooding, which lasts 45-61 days, appears to be dependent on water temperature. Nocturnal hatching, which goes on for 3-5 successive nights, apparently reduces predation on newly hatched larvae. Females die following egg brooding and hatching.

Males develop extra large suckers at the level of the seventh and eighth pair of suckers (from the mouth) about 7-9 months after settling.

For both sexes, the average natural lifespan appears to be 12-15 months. The maximum size reached is associated with feeding and size is attained for the female when the ovaries enlarge and for the male after maximum sucker enlargement. Gonad and sucker development appear to be correlated primarily to age (Van Heukelem 1973).

Larvae are free swimming and pelagic for an undetermined time before settlement. Young settle from the plankton at a body length of about 1 cm and a weight of about 0.33 g (Wells and Wells 1970).

The growth of *O. cyanea* is expressed as:

$$W = 1.28 \times 10^{-6} X^{3.92},$$

where W = weight (g) and X = age in days (Van Heukelem 1973). A reasonable estimate of age can thus be calculated from weight at capture using the above expression.

The diet consists primarily of crustaceans and rarely fish (Van Heukelem 1966). Gastropods may also be included in the diet as evidenced by the use of cowrie shell octopus lures by fishermen. The crepuscular hunting methods of hee comprise either pouncing or grabbing prey with the arms (Yarnall 1969). The octopus then either paralyzes the prey with cephalotoxin from the posterior salivary gland or physically pulls the animal out of its shell. To paralyze prey, the octopus either bites with its beak or rasps through the shell using its radula before injecting cephalotoxin (Wodinsky 1969).

Octopus are high level predators in the food chain, preying on crustaceans, molluscs, and occasionally fishes. In turn, they are the prey of a variety of fishes, seals, and man. In the NWHI, octopus constitutes a major part of the diet of the endangered Hawaiian monk seal (Gilmartin 1983). Octopus have also been found to be in the diet of many of the larger predatory fishes found throughout the Hawaiian Archipelago.

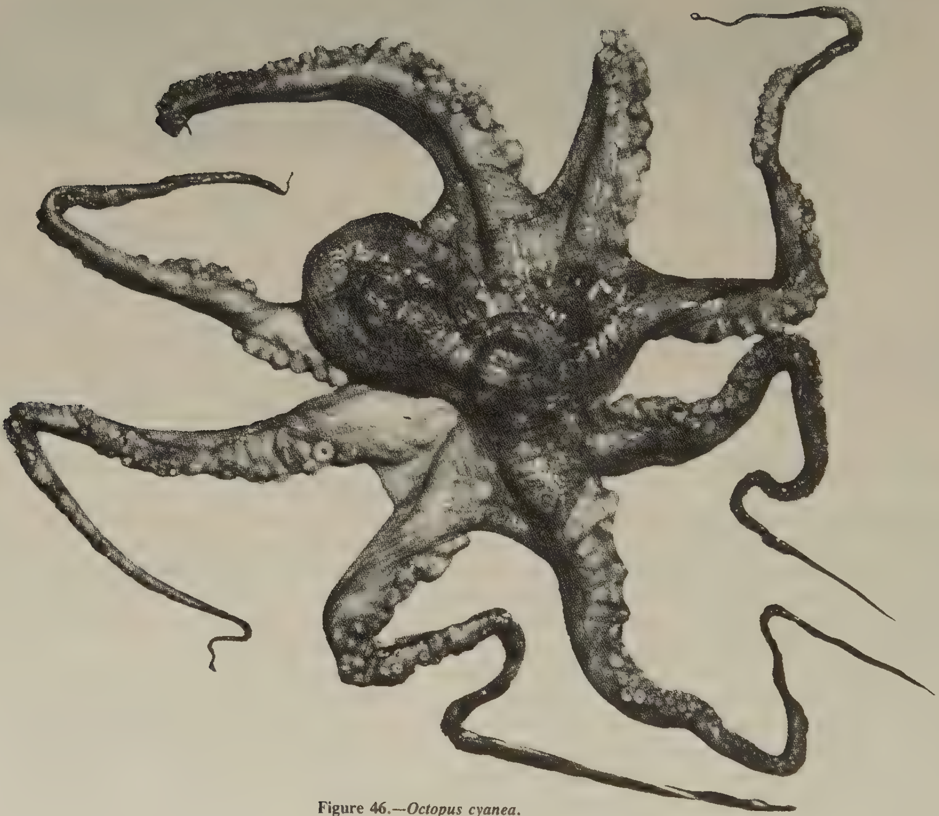

Figure 46.—*Octopus cyanea*.

Gear and catch

There is no major fishery for octopus in Hawaii. In the NWHI, most are caught incidentally in fish and shrimp traps. In the main islands octopuses are caught using spears, traps, and lures. During 1961-79, the annual landings varied between 1,722 and 10,988 kg and averaged 4,611 kg. Since octopus occurs in abundance in the inshore area, recreational harvest probably exceeds reported commercial landings. Octopus is seasonally abundant and most of the catch is made during the summer and fall months.[6]

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[6] Okamoto, H. Aquatic Biologist, Department of Land and Natural Resources, Division of Aquatic Resources, Honolulu, HI 96813, pers. commun. December 1984.

SCOMBRIDAE

8650

Wahoo

by Steven H. Kramer

Valid name	*Acanthocybium solandri* (Cuvier 1831) (Fig. 71)
Synonymy	*Cybium Solandri* Cuvier 1831 *Scomber lanceolatus* (Solander) Cuvier 1831 *Cybium sara* Lay and Bennet 1839 *Cybium petus* Poey 1868 *Acanthocybium petus* Poey 1868 *Cybium verany* Doderlain 1872 *Acanthocybium solandri* Jordan 1884 *Acanthocybium forbesi* Seale 1912 *Acanthocybium sara* Kishinouye 1915 *Scomber amarui* Curtis 1938 *Acanthocybrium solandri* Copley 1952 (misspelled) (from Jones and Silas 1964)
Common and vernacular names	Wahoo; ono

Distribution

Occurs widely in open ocean around the main islands. Present from Nihoa to Kure Atoll in the NWHI at depths from the surface to 183 m. Adult wahoo epipelagic and usually associates with banks, pinnacles, and islands; also found around flotsam far out at sea.

Distinguishing characteristics

D. XXIII-XXVII, III, 9-10+8-10; A. III, 9-10+8-9. Unique among the scombrids in having reticulated gills and lacking gill rakers. Body elongate and semifusiform, covered with small lanceolate scales. Head long, tapering to a conical snout from which the lower jaw projects slightly. Dentition consists of approximately 50 laterally compressed, slightly serrated, triangular teeth in a single series which increase in size posteriorly (Jones and Silas 1964).

Intermuscular bones inserted on ribs. First dorsal approximately uniform in height when erect. Pectorals short, reaching to below the 10th dorsal spine. Lateral line strongly arched under the 17th dorsal spine. Numerous branches extend dorsoventrally along the lateral line. Caudal fin lunate.

In life dark blue dorsally becoming silver ventrally. On young or stressed fish, 24-30 irregular dark blue vertical bars laterally on body.

Life history

Wahoo appears to spawn year round in the tropics and during the summer months in the higher latitudes, including Hawaii, as evidenced by dates and locations of larval collection in the central Pacific (Matsumoto 1967). Size at maturity is undetermined, although immature fish as large as 63 cm have been found in NMFS samples. In a preliminary study, gonad development was found to be highly heterogeneous with entirely different ova development laterally and longitudinally.[21]

Wahoo of about 131 cm spawns an estimated 6.1 million eggs per spawning (Iversen and Yoshida 1957). This compares favorably with an estimate of 6.9 million eggs per spawning for a 139-cm fish from the Gulf of Mexico.[22] Larvae are free floating and are found near and far from land. The number of spawnings per year remains undetermined.

In the NWHI, wahoo feeds on fish, cephalopods, and to a small extent, crustaceans.[23] Fish are the major prey items; *Decapterus* sp., Scombridae, and Balistidae most frequently occur in the diet. Cephalopods consist mostly of squid and to a lesser degree octopus. Crab megalops and stomatopods represent the small portion of crustaceans in the wahoo diet. It appears that wahoo forages on open water, outer reef, and flotsam-associated prey. Time of feeding is undetermined.

Wahoo are parasitized by copepods externally and trematodes and nematodes internally. The giant trematodes found posteriorly in the stomach have been identified as *Hirudinella ventricosa* (Nigrelli and Stunkard 1947).

Based on counts of daily growth rings on otoliths taken from five fish in the NWHI, the growth was linear for the size range examined (63-131 cm FL). The model predicts an age of 1 year for a fish 50.6 cm and 2 years for one 121.7 cm.[24]

The length-weight relationship of 139 wahoo from the NWHI is:

$$W = 3.55 \times 10^{-7} L^{3.5839},$$

where W = weight (kg) and L = fork length (cm). The large exponent, 3.5839, is approximately equivalent to the 3.50583 for wahoo in the Line Islands (Iversen and Yoshida 1957). Both reflect the elongate fusiform body of wahoo.

Wahoo is a high-level predator, preying on fish and cephalopods. In turn, the wahoo infrequently becomes the prey of billfish such as the sailfish, *Istiophorus americanus* (Beardsley et al. 1972). It

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[21] Prescott, J. H., Fishery Biologist, Department of Primary Industry, Fisheries Research Station, P. O. Box 5, Daru, Western Province, Papua New Guinea, pers. commun. April 1982.

[22] Finucane, J. H., Southeast Fish. Cent. Panama City Lab., Natl. Mar. Fish. Serv., NOAA, Panama City, FL 32407, pers. commun. August 1980.

[23] Kramer, S. H. Diet of the wahoo, *Acanthocybium solandri* (Cuvier and Valenciennes), in the Northwestern Hawaiian Islands. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396 (manuscr. in prep.).

[24] Uchiyama, J. H., Fishery Biologist, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, pers. commun. April 1982.

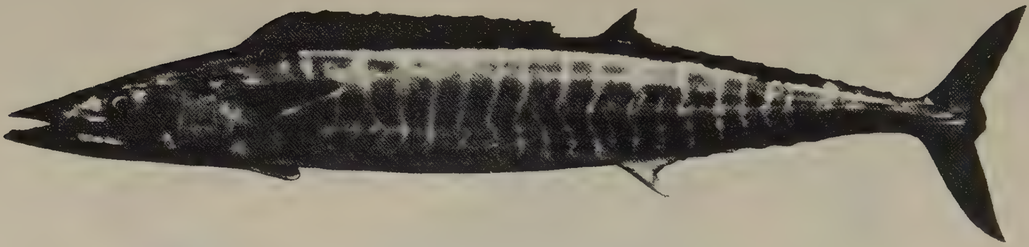

Figure 71.—*Acanthocybium solandri.*

is also conceivable that wahoo may fall prey to sharks of the Family Lamnidae or other fast-swimming predators. Juveniles may also be cannibalized by adults.[25]

Gear and catch

The species is caught principally by trolling and longline. Wahoo does not constitute a major fishery anywhere. In American Samoa, wahoo is landed as an incidental catch of the longline fishery and is canned, primarily for local consumption.

In Hawaii, wahoo is sold fresh. Annual landings in 1961-79 ranged from 10,093 to 101,347 kg and averaged 34,773 kg. Although wahoo is not a major species in the Hawaiian fishery, it is nonetheless an important food and sport fish. In recent years, the trend in catch of wahoo has been upward in response to an ever-increasing demand for the species. Many vessels now fishing in the NWHI troll for wahoo before returning to Honolulu.

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[25] Kikkawa, B. T., Research Assistant, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, pers. commun. April 1982.

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APPLICATIONS OF SATELLITE REMOTE SENSING TO FISHERIES

R. Michael LAURS*

The use of satellite remote sensing to provide synoptic measurements of the ocean is becoming increasingly important in fisheries applications. Variations in ocean conditions play key roles in natural fluctuations of fish stocks and in their vulnerability to harvesting. Information on the changing ocean, rather than on average ocean conditions, is necessary to understand and eventually to predict the effects of the marine environment on fish populations. The evolving capabilities of satellite sensor and data-processing technology, combined with conventional data collection techniques, provide a powerful tool toward ensuring the wise use of living marine resources.

Laurs and Brucks (1985) review fisheries applications of satellite oceanic remote sensing in the United States. Examples of recent and potential uses of satellite imagery in U. S. fisheries in the eastern North Pacific are given in Fiedler et al. (1985). Yamanaka (1982) describes the utilization of satellite imagery in Japanese fisheries. Gower (1982) gives an overview of the different kinds of remote sensing data relevant to fisheries science and oceanography, and Montgomery (1981) discusses the utility of satellite imagery to ocean industries, including fisheries.

Satellite Data Sources and Limitations

Satellite remote sensing applications in U. S. fisheries have concentrated on the measurements of ocean temperature and color, and computation of ocean transport based on satellite measured wind stress.

Ocean temperature

Virtually all fisheries studies employing satellite ocean temperature measurements have utilized imagery from thermal infrared sensors. The advanced infrared sensors, notably the Advanced Very High Resolution Radiometer (AVHRR) aboard the TIROS orbiting meteorological satellites, are characterized by high sensitivity in narrow wave lengths, fine ground resolution, and an extensive data archive (Fiedler et al., 1985). These sensors yield high quality data which except for some limitations, meet the requirements for most fishery investigations (Laurs, 1985).

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There have been a very limited number of attempts to apply ocean temperature measurements made from microwave instruments aboard satellites to fisheries studies. These attempts have been only marginally successful, mostly because of the large footprint of the measurements and the contamination of the data in the vicinity of land. However, an adequate evaluation of the utility of satellite microwave ocean temperature measurements in fisheries problems has yet to be conducted. Efforts to do so have been hampered because of difficulties in obtaining microwave temperature data and lack of high speed data processing capabilities to process it (Niebaur, pers. comm.)

Ocean color

The Coastal Zone Color Scanner (CZCS) on board the Nimbus-7 satellite, launched in October 1978, is the first sensor in orbit that is specifically designed to measure ocean color (Hovis et al., 1980). The CZCS is capable of measuring very subtle variations in water color resulting primarily from variations in phytoplankton concentrations. Ocean color measurements from the CZCS are being used in fishery resource applications to determine the locations of oceanic fronts, effluents, and water masses; to determine circulation patterns; and to make quantitative measurements of chlorophyll and sestonic concentrations.

Ocean winds

The scatterometer (SASS) aboard the Seasat-A satellite provided data which demonstrate the importance to fisheries of high resolution surface wind stress measurements made from space. Wind stress measurements made by satellite can be used to calculate ocean surface layer transport, which controls the distribution of larval stages and the subsequent recruitment and harvests of many marine fishes and shrimps (Brucks et al., in press). Satellite measurements of winds are also important in the detection of wind conditions that affect the safety and performance of fishing vessels at sea. Although the data record of satellite measured winds is very limited as a result of the unfortunate premature failure of the Seasat satellite, extensive global coverage of oceanic surface winds will be made by satellite systems planned for launch in the late 1980s.

Data limitations

The major inadequacy of present satellite sensors that make measurements in the visible and infrared bands is that they can measure sea surface temperature and ocean color only through a cloud-free atmosphere. This has hampered the utilization and acceptance of satellite technology in fisheries research and fish harvesting applications because many important fisheries are located in areas which have dense cloud cover much of the time.

Fiedler et al. (1985) examined the seasonal and areal distribution of cloud conditions over the eastern North Pacific and discussed the probabilities of conditions suitable for satellite coverage. They found that off the coast of Baja and California from latitude 30° to 38°N the most favorable conditions for remote sensing are from October through April, whereas a dense layer of low stratus clouds covers the coastal waters during the summer upwelling season. Off the coast of northern California, Oregon, and Washington from latitude 40° to 50°N the best conditions for remote sensing occur from August to October. North of latitude 50°N mean cloud over increases and is consistently 70% or greater in the Gulf of Alaska although March and April may be relatively clear.

Another draw back to satellite infrared temperature and ocean color measurements is their restriction to the upper most layer of the ocean surface. Although AVHRR measurements are often representative of general temperature conditions in the upper mixed layer (Bernstein, 1977), many important species live below the thermocline or on the bottom, where temperature patterns are not necessarily apparent at the surface. Another shortcoming of infrared imagery is that its use to detect fronts in open ocean areas may be limited to periods prior to the onset of seasonal warming. The use of ocean color imagery from the CZCS can often circumvent this problem (Laurs et al. 1984).

In spite of the limitations noted, data from the CZCS and advanced infrared sensors on satellites meet the general needs for many fisheries applications. The development of reliable microwave radiometers that can measure sea surface temperature with high resolution through clouds, along with advanced infrared sensors, however, is required to make full utilization in fisheries of ocean temperatures measured from space.

While the requirements of satellite sensor measurements for fisheries applications have been treated extensively (e. g., Sherman, 1980) specification of requirements for ground processing and data delivery systems have been neglected and require further development. There are pressing needs to increase the availability of ocean measurements made by satellite for use in fisheries applications. In some cases, direct reception and processing of the satellite data are required. In others the routine distribution of earth-located and geographically rectified charts of level 3 data will suffice.

Use of Satellite Measurements in Fisheries Research

Variations in environmental conditions affect the recruitment, distribution, abundance, and availability of fishery resources. It is not possible to measure remotely from satellites the entire spectrum of information needed to assess changes in the marine environment. However, knowledge of important oceanographic conditions and processes affecting fish populations may often be deduced using ocean measurements made by satellite, e. g., distribution of surface isotherms, locations of oceanic frontal boundaries, information on currents and circulation patterns, regions of upwelling, and so on.

Measurement of marine fish habitat

Ocean measurements made by satellite remote sensing can be extremely useful in defining the distribution of marine fish habitats. Lasker et al. (1981) and Fiedler (1983) have demonstrated that the northern boundary of northern anchovy spawning habitat in the Southern California Bight may be delimited using AVHRR imagery from NOAA polar orbiting satellites. In general, the northern extent of spawning in the Bight and the offshore extent of spawning north of Santa Catalina Island are limited by cold, upwelled waters advected south of Point Conception. The cold waters are readily evident in satellite infrared imagery of the region (Fig. 2). The southern limit of spawning may be defined using ocean color measurements made by the CZCS aboard the Nimbus-7 satellite showing low chlorophyll concentrations (Fiedler, 1983).

The distribution and availability of albacore tuna off the west coast of the United States have been found to be related to oceanic fronts seen in AVHRR infrared and CZCS imagery (Laurs et al. 1984). Commercially fishable aggregations of albacore are found in warm, blue oceanic waters near temperature and color fronts on the seaward edge of coastal water masses (Figs. 4 and 5). These oceanic boundary features, which are believed to result primarily from coastal upwelling, are clearly observable in satellite imagery collected along the U. S. Pacific coast. The distribution of albacore during winter time in regions hundreds of miles off the coast has also been related to sea surfaçe temperature fronts, believed to mark the outer boundary of the California Current observed in AVHRR imagery (Laurs et al. 1981).

The small-scale migration patterns of albacore in relation to oceanic frontal boundaries was investigated using ocean color and infrared data collected contemporaneously with observations made from ships at sea by Laurs and Austin (in press). Nimbus-7 CZCS and NOAA-6 satellite AVHRR infrared data were collected in conjunction with field experiments where acoustic telemetering was used to track the horizontal and vertical movements of free-swimming albacore, and expendable bathythermograph (XBT) observations were made to determine subsurface ocean thermal structure. Three albacore were tracked for approximately 24 hr and one for about 15 hr. The results showed that (1) total distances tracked ranged rom about 40 to 60 km, with all fish remaining in the same parcel of warm water that was separated from waters to the north, south, and inshore by about a 2°C temperature gradient as shown by infrared thermal imagery ; (2) tracked fish spent most of the time in waters within and below the thermocline, and only small amounts of time in the upper mixed layer (Fig. 6) ; (3) the fish exhibited marked vertical excursions in depth with the range being larger during the day than at night ; (4) the fish spent most time in waters with temperatures considerably lower than what has been generally believed to be the preferred temperature range for albacore ; and (5) when changing depth, the fish frequently within a 20-min period, passed through a vertical gradient of temperature amounting to 6-7°C or about 3 + times greater than the horizontal temperature gradient at the surface indicated by ship measurements and the infrared thermal imagery. These findings indicate that the reasons tuna aggregate on the warm side of surface temperature fronts-an economically significant phenomenon that has been observed on scientific cruises and is well known by fishermen - may not be related to thermal-physiological mechanisms (Neill. 1976). Instead, water clarity as it affects the ability of time to detect prey may be in an underlying mechanism.

Satellite infrared measurements have also been used to trace the development and duration of the various bluefin tuna fisheries along the east coast of the United States (Roffer et al. 1982). These fisheries follow the movement of seasonal warming of near-surface waters which are monitored by observing the northerly progression of the 19-20°C isotherms in satellite infrared imagery. Limited success has been achieved during winter months in relating the distribution of tuna longline fishing in the Gulf of Mexico with position of the Loop Current deduced from temperature frontal patterns observed in Geostationary Orbiting Earth Satellite (GOES) infrared imagery (Leming, Internal Report, NMFS and Maul et al., 1984). In summer months after seasonal warming has occurred, it is not possible to resolve temperature frontal structure in the GOES infrared imagery of the Gulf of Mexico.

Satellite remote sensing has been an especially important tool during the recent El Niño for monitoring anomalous ocean conditions along the U. S. Pacific coast (Fiedler, 1984a). The satellite imagery contains invaluable information for use in assessing the effects of the El Niño conditions on U. S. west coast fisheries. Virtually all of the fisheries were affected in varying degrees, with some fisheries showing benefits from the El Niño and others being harmed substantially. Many fish populations experienced changes in their distribution and centers of abundances. For example, there were shifts in the usual distribution of anchovy spawning which Fiedler (1984b) found could be delineated using AVHRR infrared imagery.

Use of satellite in design of field studies and interporetation of ship data

Another area where satellite data are being used in fisheries research is to assist in the design of field studies and to guide research operations on fishery research vessels. This has been an extremely important use of satellite data at the National Marine Fisheries Service Southwest Fisheries Center. Satellite data are used in planning sampling patterns and cruise tracks, to make adjustments in cruise operations while at sea, and to assist in the intrepretation of cruise results. The use of satellite measurements has markedly enhanced sampling ability, enabling researchers to sample the right places at the right times and has resulted in considerable savings in time and funds. This important application of satellite remote sensing usually requires direct reception and processing of satellite data in near real time. The cost savings for conducting research can be significant, since a single satellite image from data received and processed in a matter of a few hours can save days of expensive ship time by locating significant ocean feature and permitting optimum sampling effort (Fiedler et al., 1985). It can be used to validate the interpolation and extrapolation of shipboard measurement and as the basis for interpretation of measurable patterns and possible mechanism responsible for spatial and temporal variability observed in shipboard observations (LASKER et al. 1981).

Potential use of satellite data in fisheries studies

There are a number of fishery research situations where satellite data can potentially play an important part in the future. For example, satellite measurements can provide vast amounts of oceanographic data for use in evaluating the status of fish stocks as advanced models for fishery stock assessment are developed which incorporate environmental information. Investigations concerned with determining interactions between fisheries and pollution are prime candidates for the use of satellite ocean measurements. For example, ocean color and other imagery can be used to determine dispersion patterns of waste dumped at sea. Satellite measurements of ocean chlorophyll also may be extremely useful in studies to model ecosystem energy budget to estimate potential fish stock production.

Use of Satellite Measurements in Fisheries-Aid Products for Fishermen

Several projects and programs have used or are using satellite-derived ocean data in fisheries-aid products which are distributed to U. S. fishermen by a variety of mechanisms, including radio facsimile transmission, voice broadcast, U. S. mail, and telephone telecopier. A prime motivation leading to the expanded use of satellite observations in fisheries-aid products was provided by the Seasat Commercial Demonstration Program sponsored by the National Aeronautics and Space Administration/Jet Propulsion Laboratory in Pasadena, California. This program led to the development of an operational Satellite Data Distribution System used to distribute oceanographic products to ocean users (Montgomery, 1981).

Charts showing the locations of oceanic thermal boundaries are derived from AVHRR infrared imagery from polar orbiting satellites and are provided to commercial and recreational fishermen for use in locating potentially productive fishing grounds along the Pacific coast from central Baja California to British Columbia, Canada (Breaker, 1981). Fishermen use these charts to save time in searching for productive fishing areas associated with oceanic frontal features. High resolution infrared images from the GOES satellite and ship reports are used in the preparation of charts for waters off the Atlantic Coast, which are distributed to fishermen and other marine users (Chamberlain, 1981). Of particular interest to fishermen, these charts show the outer limit of the shelf water mass, in which many fishery resource species reside. The charts also give information on the numbers, sizes, and persistence of warmcore Gulf Stream rings, which can markedly alter conditions on the fishing grounds. These charts have been particularly useful to lobster fishermen in reducing loss of fishing pots as a result of strong currents of the Gulf Stream warmcore eddies. Charts based on GOES infrared imagery are also prepared to show the path of the Loop Current in the Gulf of Mexico and are used mostly by recreational fishermen (Lowry and Leaky, 1982).

Experimental ocean color boundary charts based on CZCS imagery are distributed to U. S. westcoast fishermen (Montgomery, 1981). These charts delienate strong gradients in the blue/green color ratio (Channel 1/channel 3 radiances). They are produced at almost weekly intervals depending on cloud conditions. and cover coastal areas up to 700,000 km² between Guadalupe Island and Vancouver Island. Nimbus-7 CZCS passes along the Pacific coast are collected at the Scripps Institution of Oceanography (SIO) Satellite Oceanography and transmitted by radiofacsimile the following day to fishing boats at sea from radio station WWD in La Jolla, California. Color photographs of the satellite images are also distributed by express mail to various fishing ports and to Sea Grant marine advisors in daily contact with fishermen. The color boundary charts and photographs are used primarily by commercial albacore swordfish and salmon fishermen, and recreational fishermen in southern California. Fishermen use the color boundary charts to locate color gradients or "breaks" which are important in determining potentially productive fishing areas.

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衛星リモートセンシングの米国漁業への応用

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摘　要

衛星データ・ソースとその限界

米国漁業への衛星の応用は水温，水色，および衛星によって測定された風のストレスから輸送を計算することに力が注がれている。

水温：AVHRR は，波長帯の幅が狭く高感度で地上分解能がすぐれ，データの蓄積も多く，幾つかの問題点はあるが，漁業調査の要望の大部分に応えている。

マイクロウェーブによる水温測定の企てはまだ多くない。それは地上分解能が悪く，陸に近いところではコンタミネーションがあり，またデータの高速処理能力に問題があるためである。しかし漁業のために衛星のマイクロ波による水温情報を応用する研究は今後も行わなければならない。

水色：NIMBUS-7 の CZCS は主に植物プランクトンによる水色の微細な相違を測定できる。これは前線，流出，水塊などの位置の探査，環流のパターン，クロロフィル量の測定など水産資源に対して応用されつつある。

海風：Seasat-A に搭載された散乱計 (SASS) により海上の風の正確な測定が漁業に大切であることが示された。これは稚魚の輸送や加入，漁獲などに影響する表層の輸送を求めるのに応用することができる。また衛星からの風の測定は言うまでもなく漁船の安全にも重要である。Seasat は寿命が短く，そのためデータの蓄積は少ないが1980年代後半には衛星による地球的規模での風のデータを集めるシステムが出来よう。

データの限界：現在のセンサーの第一の限界性は雲のないところでないと用いられないことである。これについては季節による雲量分布が調査された。

いま一つの障害は衛星資料が表面に限られることである。AVHRR は上部混合層迄の状態を示すことがしばしばあるが，生物のあるものはこれよりも深いところに住んでいる。

また外洋では，赤外画像で前線を見ることができるのは，夏季の水温上昇の始まる前に限られることである。これは CZCS による水色で補うことができる。

このようにいろいろの限界はあるが，AVHRR と CZCS の併用により漁業の問題の多くに対応することができるが，更に雲を透して水温を高精度で測定するマイクロ波センサーの進歩が望まれる。

センサーによる測定の漁業に対する要望に比べ，地上での資料処理，およびその伝達法に関する要望には立ち遅れがある。船上での直接受信・処理の要望もあるが，地上で作成し，地理補正をした図面の配布で十分なこともある。

漁業研究における衛星測定の応用

魚の生態に関係する海洋環境のすべてを衛星によって観測することは出来ないが，等温線，前線のような重要な海況は衛星資料から判断することができる。

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海中の魚の行動の測定例

カタクチイワシ：南カリフォルニア湾での産卵の北限は Point Conception の南にある湧昇冷水で規定されるが，これは AVHRR 画像で明瞭に示される。また，その南限は CZCS による水色測定で，クロロフィルの少ない海域として識別できる。

ビンナガ：米国西海岸沖の漁場は沿岸水塊の沖側の水温および水色の境界に近い高温で青い外洋水にできる。この前線は沿岸湧昇によるものであり，衛星の AVHRR，CZCS 画像等によって明らかにみることができる。冬季にはビンナガの分布はやはり AVHRR でみられる遙か沖のカリフォルニア海流の外側の温度前線と関係をもっている。

CZCS および AVHR のデータにあわせて XBT による中層水温測定や音響テレメトリーを船上で行うことによりビンナガの小規模の回遊の有様が調査された。3尾のビンナガを24時間，1尾を15時間追跡したが，どれも赤外画像で判断される約2°Cの水温傾度によって判別される同一暖水塊にとどまること，魚は大部分の時間は温度躍層の内部またはその下部にいること，上下移動は夜間よりも日中で激しいこと，従来考えられていたよりもかなり低温な水域で過ごすこと，この場合，衛星や船舶資料によりみられる水温水平傾度の3倍以上もある6～7°Cの水温差を20分以内で乗り越えることなどがしられた。

クロマグロ：大西洋岸の春のクロマグロの北上は，赤外画像で示される19～20°Cの等温線の移動に従っている。冬のメキシコ湾では静止衛星 GOES による水温前線から判断された環状流（Loop Current）に関係した位置で，はえなわがある程度成功しているが，夏にはこの衛星の赤外画像では温度前線は判別できない。

エルニーニョ：殆ど総ての魚種がエルニーニョによって好影響，または悪影響をうけた。たとえば，カタクチイワシの産卵場の著しい移動があったがこれは AVHRR の画像により，水温変動が明らかに認められた。

海上調査の設計および船舶データの解釈に対する衛星の応用：

これは南西漁業センターにおける衛星の極めて重要な応用の1である。即ち，調査航路，観測点の位置，時間などを正しく定めることにより，労力と経費を節減できる。このためには，衛星資料の直接受信およびリアルタイム処理が必要であるが，一枚の画像処理に数時間かかっても，これは数日間の調査日数や労力の節減になる。また衛星データは船舶データを内挿，または外挿して海況の時空的分布をより正確に解釈するに用いられる。

衛星の漁業研究に対する今後の応用：例を挙げれば，資源評価に環境情報を組み合わせるときには衛星は膨大な海洋データを提供できる。また漁業と海洋汚染との関係の研究は衛星応用に期待される一つである。海に排出された汚染物資の拡散は水色その他の画像で観察できる。漁業資源の可能生産量を推定するための生態系エネルギー収支モデルの研究には衛星によるクロロフィルの測定が極めて重要である。

漁業者に対する情報サービスにおける衛星の応用：米国では衛星による海洋データを無線ファックス，無線電話，郵便，電話ファックスなどを用い漁業者に配布するいくつかのプロジェクトがある。衛星データを漁業情報に応用するための最初の動きは NASA と JPL（ジェット推進研究所）により推進された Seasat Commercial Demonstration Program で，これは海洋データの産出物を海洋ユーザーに提供する実用システムの開発をもたらした。

太平洋岸では AVHRR による温度前線の位置が漁場の探査のために商業漁業者や遊漁者に提供され，漁場探査の時間の節減に役立っている。

大西洋岸では GOES 衛星の高分解赤外画像と船舶資料による海況図が漁業者その他に提供されている。この海況図は多くの水産資源生物が住んでいる陸棚水の外縁を示すので漁業者の関心が高い。また，この図はロブスター漁業者にとっては

メキシコ湾流の暖水渦による強い流れのために生ずる漁具の損失を軽減するのに極めて有用である。また，前に述べたとおりメキシコ湾内の環状流（Loop Current）の流路を示す図が作られて漁業者に用いられている。

CZCSの青（第1バンド）と緑（第3バンド）との比を用いた水色前線図は，雲の状態にもよるが殆ど毎週1度の割りで太平洋側の漁業者に配布されている。太平洋岸を通過するNIMBUS-7，CZCSはスクリプス海洋学研究所で受信され，その翌日，研究所の無線局から漁船に放送されるほか，画像のカラー写真は速達郵便で漁港に送付される。これらの水色前線図やカラー写真はビンナガ，メカジキ，サケ等の商業漁業者や，南カリフォルニアの遊漁者が生産力の有望な漁場を求めるのに利用されている。

註：本報告は昭和60年6月に日本大学会館で行われた講演の内容に若干の補筆をしたものを著者から本紙に特別寄稿されたものである。

尚写真等は、送付が本号印刷に間に合わなかったので割愛した。

抄訳　山中一郎

8652

Pen Rearing Pacific Salmon, *Oncorhynchus* spp., in San Francisco Bay

WILLIAM S. LEET, ROGER E. GREEN, and DANIEL RALPH

ABSTRACT—Chinook, Oncorhynchus tshawytscha, *and coho,* O. kisutch, *salmon were pen-reared in San Francisco Bay from 1974 to 1979 at the NMFS Southwest Fisheries Center's Tiburon Laboratory, Tiburon, Calif. Environmental and experimental conditions varied from year to year and tag returns indicated an inconsistent contribution of the different pen-reared groups to the local sport fishery and ocean harvest. The best results were from chinook salmon reared in 1976. Although commercial applications of pen rearing in San Francisco Bay might succeed, we do not see the release of pen-reared fish as an effective management technique for increasing the ocean catch in California.*

Introduction

Saltwater net-pen culture of Pacific salmon, *Oncorhynchus* spp., is a recent development in salmonid management. The technique consists of transferring smolts directly from fresh water into saltwater net pens. The salmon are reared in salt water, where their growth rate is accelerated, and at the appropriate time or size of fish, they are released or harvested for marketing.

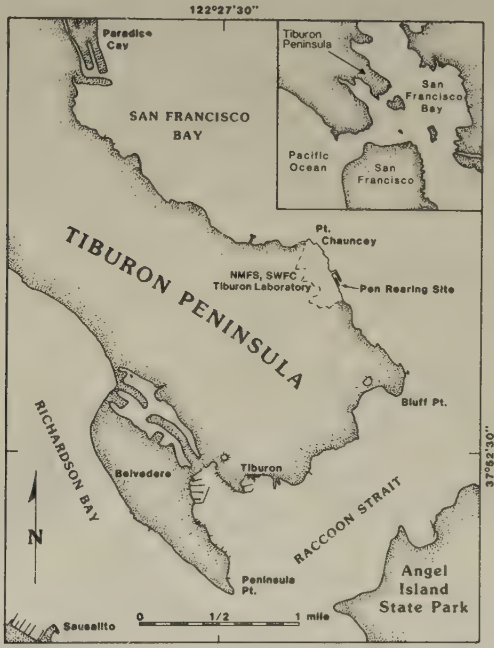
122°27'30"
Paradise Cay
SAN FRANCISCO BAY
Tiburon Peninsula
San Francisco Bay
Pacific Ocean
San Francisco
Pt. Chauncey
TIBURON PENINSULA
NMFS, SWFC Tiburon Laboratory
Pen Rearing Site
Bluff Pt.
RICHARDSON BAY
Belvedere
Tiburon
37°52'30"
N
RACCOON STRAIT
Peninsula Pt.
Angel Island State Park
Sausalito
0
1/2
1 mile

Figure 1.—Pacific salmon pen-rearing study area.

Research on saltwater pen rearing on the U.S. west coast was initiated in 1969 by the National Marine Fisheries Service's (NMFS) Northwest and Alaska Fisheries Center at its Manchester Field Station on Clam Bay in Puget Sound, Wash. (Novotny, 1975). Coho, *O. kisutch*, and chinook, *O. tshawytscha*, salmon held in saltwater net pens in Puget Sound beyond the time of their normal migration into the sea tended to remain in the Sound and were more accessible to recreational fishermen (Novotny, 1975; Moring, 1976). In addition, chinook salmon were found to return to streams closest to the pen-rearing site rather than to their natal or hatchery streams (Novotny, 1975). Such delayed release of pen-reared salmon resulted in improved returns to the fishery as well as better spawning escapement (Mahnken and Joyner, 1973).

The Squaxin Indian tribe, Shelton, Wash., has pen-reared coho salmon since 1976 and is currently releasing over 1 million fish annually. This program has increased the tribal catch dramatically. Consistent returns of 15-20 percent are being achieved[1].

In 1974, the NMFS Southwest Fisheries Center's Tiburon Laboratory, Tiburon, Calif. (Fig. 1), in cooperation with the San Francisco Tyee Club (a

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[1] Tim Tynan, Squaxin Indian Tribe, Shelton, Wash. Unpubl. data.

recreational fishermen's association), the California Department of Fish and Game (CDFG) and the University of California Cooperative Extension Service—Sea Grant (UCSG) began a series of salmon pen-rearing and release experiments to investigate the feasibility of pen rearing in San Francisco Bay. The primary objectives were to learn if seawater pen rearing of Pacific salmon would be possible in San Francisco Bay and if a recreational coho fishery could be established inside the Bay. As the study progressed, we added the ancillary objectives of measuring the contribution of pen-reared salmon to the ocean harvest and determining if pen rearing salmon in San Francisco Bay would be a cost-effective technique for augmenting the ocean harvest of Pacific salmon.

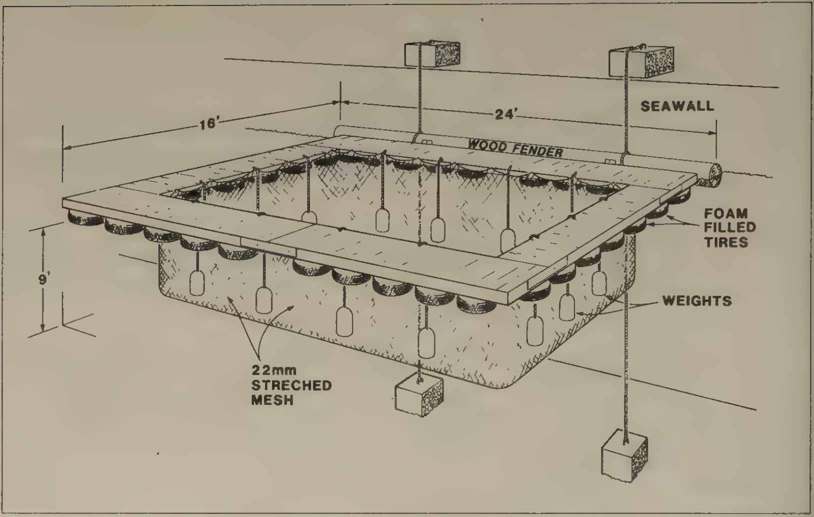

Figure 2.—Diagram of rearing pen.

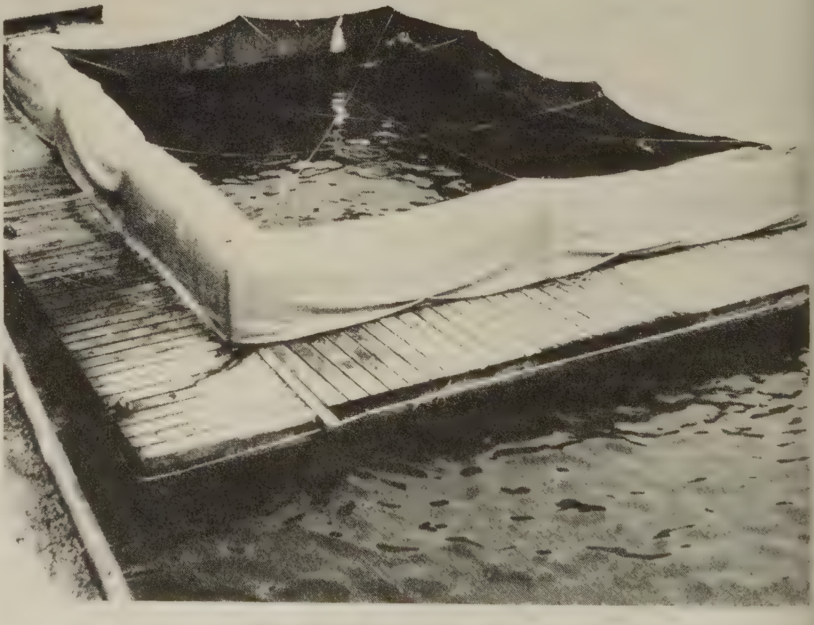

Figure 3.—Rearing pen in place.

Rearing Environment

The pen-rearing site at the Tiburon Laboratory was on the northeast shore of the Tiburon Peninsula on San Francisco Bay (Fig. 1). The pens were fastened alongside a concrete quay where the depth was 3.2 m at mean lower low tide and the mean daily tidal range was 1.75 m. Tidal currents typically reached 1 km/hour. The pens were exposed to wave action from wakes of passing ships and from wind waves ranging up to 1.6 m. Annual ranges in salinity and temperature recorded at the pen-rearing site were 9-31‰ and 9.5°-21.0°C, respectively.

Net-pen enclosures, constructed of nylon mesh in the form of topless rectangular boxes, were hung from floats which also served as walkways (Fig. 2, 3). Mesh sizes were 22-32 mm stretched measure. To prevent deformation of the net in tidal currents, plastic gallon jugs filled with sand were suspended from lines inside each corner, and at about 1.8 m intervals along the sides and ends.

Predaceous seabirds were excluded from the open tops of the net pens by nylon nets stretched over the pens about 1 m high on pipe stanchions and polypropylene rope crisscrossed over the pen structure.

Pen-Rearing Procedures

Table 1 summarizes information on the nine groups of salmon reared during the study. Coho salmon were initially selected for the pen-rearing experiments on the basis of the NMFS Manchester Field Station reports and the evaluation guidelines given by Novotny

Table 1.—Summary of details pertaining to Pacific salmon pen-reared and released at the Tiburon Laboratory, 1974-79.

Group no.	Species	Brood stock	Last hatchery	No. fish delivered	Release date	Days in pen	No. fish released	Mean size (g/fish) at delivery	Mean size (g/fish) at release
1	Coho	Noyo R., Calif.	Mad R., Calif.	10,000	11/06/74	119	4,000	15	200
2	Coho	Kalama R., Wash	Mariculture N.W., Wash.	40,000	11/24/75	116	30,320	19	220
3	Coho	Alsea R., Oreg.	San Joaquin, Calif.	30,000	3/31/76	74	5,700	62	90
4	Chinook	Fall run Feather R., Calif.	Feather R., Calif.	20,250	12/17/76	78	6,900	34	103
5	Coho	Skagit R., Wash.	Mad R., Calif.	30,000	7/14/77	128	3,430	23	131
6	Coho	Toutle R., Wash.	Aqua Dell, Oreg.	28,250	9/12/77-11/08/77	53-110	9,220	22	86 206 233
7	Chinook	Fall run Feather R., Calif	Feather R., Calif.	100,480	6/13/78	53	24,700	3.2 3.5	7.9
8	Chinook	Fall run Feather R., Calif.	Feather R., Calif.	100,000	10/26/78, 11/03/78	129-136	19,900	6.7 8.5	68 85
9	Chinook	Fall run Feather R., Calif.	Feather R., Calif.	76,050	11/20/79, 11/21/79	92-93	12,720	14	75

Table 2.—Summary of tag release and return details for groups of salmon pen-reared at the Tiburon Laboratory, 1974-79.

Group no.	Tagged[1] fish released (no.)	Tag[1] returns (no.)	Percent return	Adjusted[2] return rate (%)
1	4,000 N 600 F	16 N 2 F	0.4 N 0.3 F	—[3] —[3]
2	7,631 C	67 C	0.9	3.9
3	4,717 C	42 C	0.9	3.9
4	2,645 C	144 C	5.4	23.5
5	2,417 C	2 C	0.1	0.4
6	6,433 C, B	13 C 0 B	0.2 C	0.8 C
7	16,300 N	275 N	1.7	—[3]
8	18,500 N 1,400 C	2,461 N 20 C	13.3 N 1.4 C	 5.9 C
9	12,720 n	1,435 N	12.8	—[3]

[1] Tag types: B = Freeze brand, C = Carlin, F = Floy dart, and N = nose.

[2] Adjusted for tagging mortality/tag shedding.

[3] The tagging mortality/tag shedding adjustment factor of 4.32 demonstrated for Carlin tags only.

(1975). These reports indicated that cohos are more resistant to disease and handling mortality during saltwater culture than chinook salmon, and exhibit good first-year growth in salt water. Also, since coho salmon are not normally found in either the Sacramento-San Joaquin River system or the San Francisco Bay-Delta system (Hallock and Fry, 1967) we could assume that most cohos found near the rearing site or upstream had originated at our net pens.

Smolts (young fish physiologically capable of osmoregulating in seawater) were provided by State or Federal hatcheries in California or were purchased from commercial hatcheries in Oregon or Washington. The fish were delivered to Tiburon by hatchery trucks usually equipped with refrigeration and recirculating pumps.

Several factors led to our decision to use chinook salmon for the final three rearing experiments. They were readily available from California State hatcheries free of charge, whereas cohos were not, and funds were not available to purchase cohos from commercial hatcheries. In addition, we had successful results with the chinooks reared in the Group 4 experiment.

Groups 1, 2, and 5 (Table 1) were inoculated against *Vibrio anguillarum* by vaccine injection at least 2 weeks before transport. Group 9 was inoculated against *V. anguillarum* by immersion in vaccine. The other groups were not inoculated.

In 1974, the first year of the pen-rearing experiments, the fish were fed Oregon Moist Pellets[2] (OMP). Thereafter, rearing capacity was quadrupled and dry-pellet salmon diets were substituted because sufficient refrigerated storage capacity for the OMP was not available.

Feeding rates of 3-5 percent body weight per day were used, dividing daily rations into four feedings. For groups with a large size range, the daily ration was divided into three feedings so that toward the end of each feeding period there was food left for the smaller, less aggressive fish after the larger ones had fed to satiation.

Pen stocking did not exceed the recommended density of 16 kg/m^3 (Novotny, 1975). As the salmon grew, fish were transfered to avoid exceeding this capacity.

After release of the salmon, nets were removed from the Bay and hung to dry. The nets were cleaned of fouling growth, inspected, and mended. At the end of the rearing year, pen sections were disassembled in the water, lifted out, and inverted for drying. When the sections were dry, the fouling organisms were scraped away and repairs were made. The work was usually accomplished in less than 100 worker-days.

Tagging

All 10,000 coho salmon of Group 1 (1974) and many chinook salmon in Groups 7, 8, and 9 were internally nose-tagged with binary-coded magnetic wire tags (Jefferts et al., 1963) and adipose-fin-clipped for field recognition (Table 2). Additionally, 600 fish from the 1974 rearing were double-tagged with plastic dart tags (Dell, 1968). Carlin tags (Saunders, 1968) were used from 1975 through 1978. Tagged fish were held in recovery pens until normal feeding behavior resumed—usually 1-2 days. Mass releases into the Bay were timed for an ebbing tide when the water was turbid to help conceal them from predators.

In addition to being Carlin-tagged, one group (Group 6) was also freeze-branded (Mighell, 1969) to test the effectiveness of this less expensive marking procedure. For this test, a 6.35 mm dual brand (symbol IH) was applied under the dorsal fin. When fish were not marked and therefore not counted, the number released was estimated by weighing and counting random samples of the fish as they were dipnetted from the pens.

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[2] Mention of trade names or commercial firms does not imply endorsement by the authors or the National Marine Fisheries Service, NOAA.

Pen-Rearing Experience by Year

Between July 1974 and November 1979, nine groups of salmon were reared and released at the Tiburon Laboratory saltwater pen site. Tables 1 and 2 summarize details of rearing and tag returns. Because of the great experimental dissimilarity among the rearing groups, we present here notes, by group, on our experiences in rearing these fish. Group numbers match those used in Tables 1 and 2.

Group 1, 1974

In the first year of the project, 10,000 coho salmon were reared in one pen as a pilot study. The fish, from Noyo River brood stock, were hatched and reared by CDFG at the Mad River Fish Hatchery, Arcata, Calif. They were injected with vibrio vaccine when they were nose-tagged at the hatchery. They were delivered to the Tiburon Laboratory and placed in a floating pen on 10 July 1974 at an average size of 15 g.

Observed mortalities in this group of fish during pen rearing were 2,845, of which about 10 percent were found on the surface. The release of an estimated 4,000 fish revealed an inventory discrepancy of 3,000 fish. The problem of unaccountable inventory losses was also prevalent in each succeeding rearing throughout the later years, and has been reported by other workers who have reared salmon in pens[3].

Group 2, 1975

This group of coho salmon was obtained from a commercial salmon grower in Washington. They had already been injection-immunized for vibriosis. On 1 August, 40,000 fish were delivered to Tiburon and placed in one net pen.

For several days, the salmon were fed a mixture of OMP and dry pellet feed sprayed with fish oil. After this adjustment period, they were fed a straight diet of dry pellets. As the salmon grew, they were transferred to other net pens until they were about equally divided among four pens. This group experienced fewer problems and greater survival during rearing than any other group. On 24 November, the 30,320 fish remaining were released; 7,631 of these were tagged.

Group 3, 1976

Yearling coho salmon were the first of two groups reared in 1976. Because the fish were delivered on short notice, the pens and nets were not ready; however, two above-ground plastic swimming pools were available for use. These pools were supplied with Bay water by a submersible pump.

On 16 January the salmon were delivered and stocked in the two pools. One net pen was made ready, and 7,500 fish were transferred to it on 4 February. That night the pump supplying the pools failed and the 22,000 fish still in the pools suffocated by the next morning.

The salmon placed in the net pen were the largest received during the entire project and had a large size range (20-270 g), as they had never been graded during their year of hatchery rearing. This presented feeding problems due to the dominance of the larger fish.

Pen rearing lasted through March, and the fish were released on 31 March. Of the 5,700 released, 4,717 had been Carlin-tagged the week before.

Group 4, 1976

Cohos were not available but 20,250 fall-run chinook salmon were obtained from the CDFG Feather River Hatchery in Oroville, Calif. These fish were just under 1 year old, and upon delivery on 1 October they averaged 34 g. They had not been vaccinated against vibriosis.

On 14 November waves broke the first pen loose from its moorings and about 12,000 salmon escaped before the net was repaired and the pen returned to its mooring. The remaining fish were unharmed.

This group, the first chinook salmon reared in the project, was healthier than most others. Size range was small and all fish appeared to feed well throughout the rearing period. They were hand-fed dry pellets four times per day at a daily ration of 4 percent of their weight. No disease problems were encountered. We were impressed by the ease of rearing and the good growth rate for this first group of chinooks, both being contrary to reports that chinook salmon were more difficult to rear than cohos. On 17 December, after 78 days of rearing, the surviving 6,900 chinooks were released, 2,645 of which were Carlin-tagged.

Group 5, 1977

These coho salmon from the Mad River Hatchery were delivered to Tiburon on 3 March. At delivery, the 30,800 fish had a mean weight of 23 g (range 10-199 g). A high incidence of cannibalism was anticipated, and was verified by observation. The cohos appeared to be in poor health at delivery and suffered heavy mortality during their confinement. At release on 14 July, only 3,430 fish remained, of which 2,417 were Carlin-tagged.

Group 6, 1977

This group consisted of coho salmon from Toutle River (Washington) brood stock reared in fresh water at Aqua Dell Farms in Oregon. A total of 28,250 salmon, averaging 22 g, was delivered to Tiburon on 21 July. Initial mortality in this group was high: 33.1 percent of the number delivered died within the first 5 days.

Freeze-branding and Carlin-tagging began on 7 September, about 1½ months after the fish were introduced into the net pen. The number of marked fish released was 6,433. These were the last coho salmon reared and released during the project.

Group 7, 1978

Chinook salmon for the 1978 and 1979 rearings were obtained from fall-run Feather River brood stock spawned and reared by CDFG at the Feather River Hatchery, Oroville, Calif. The first 1978 group was delivered to Tiburon on 21 April and consisted of about 100,480 fish, of which 38,160 were nose-tagged.

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[3] A. Novotny, NMFS Northwest and Alaska Fisheries Center, Seattle, Wash. Personal commun.

We planned to rear tagged and untagged fish in adjacent pens. However, the net pen into which the untagged fish were being stocked was of a slightly larger mesh size which allowed some of the fish to escape. After the problem was discovered, the remaining untagged fish were put into the smaller mesh pen with the tagged fish. On the third day after delivery, nose-tagged fish averaged 3.5 g and untagged fish averaged 3.2 g; these were the smallest salmon received during the project.

The fish were reared for 53 days and the 24,700 remaining after disease mortality and escape were released on 13 June. At an average weight of 7.9 g, these fish were smaller than those of any other release group. Indeed, they were smaller at release than the mean size of any other group at delivery.

Group 8, 1978

The second group of chinook salmon in 1978 was composed of 50,000 nose-tagged and 50,000 untagged fish, reared in separate pens. The nose-tagged fish were delivered on 19 June, and the untagged fish the following day. The same problem of fish escaping the pens occurred with these untagged fish as had occurred in the spring delivery; there were two distinct size modes of fish, and the smaller ones easily passed through the net. Weight samples were taken 2 days after delivery. Nose-tagged fish averaged 8.5 g and untagged fish 6.7 g.

For prophylactic treatment, Terramycin was administered in the food for 10 days, starting with the initial feeding. When the Terramycin was discontinued on 29 June, tagged fish began to die in increasing numbers, and heavy mortality occurred on 5 July. The dying fish exhibited whirling behavior, external lesions, and hemorrhaging fins.

On 7 July, live samples of tagged and untagged fish were examined at the State Fish Disease Laboratory. Preliminary diagnosis for the tagged fish was vibriosis. No disease organisms were detected in the untagged fish; however, a vitamin deficiency was found. Thereafter, Terramycin and vitamin supplements were added to the feed.

The untagged fish suffered a negligible mortality rate, but many had escaped. On 17 August the net pen with untagged fish was inventoried and at least 35,000 fish were unaccounted for. The counting process killed 25 percent of those remaining. Several factors, in particular heavy scale loss and high water temperature, may have been responsible.

The nose-tagged fish were released on 26 October. On the release date a tag-retention check was performed which indicated 98 percent retention of the coded-wire nose tag.

The remaining untagged fish were Carlin-tagged 30 October-1 November. Only 2,000 of the expected 9,600 were present in the net pen. These fish, the last to be Carlin-tagged in the project, were released on 3 November 1978.

Group 9, 1979

In the final rearing experiment, two separate groups of chinook salmon were used—one reared in net pens as in previous years and the other released at the pen site upon delivery. Each group was nose-tagged. The second group served as a control to learn the effects of saltwater rearing and delayed release on survival. Both groups received identical treatment during freshwater residence, including immersion vaccination against vibriosis. Fish were delivered on 20-22 August. Average weight of both groups at delivery was 14 g. The pen-reared group numbered 76,050 fish and the release group numbered 24,800.

Feed rations were maintained at 3 percent throughout the rearing period, and Terramycin and vitamins were added at regularly scheduled intervals. Sulfamethazine was administered for 5 days immediately following the removal of a few dead fish from two of the net pens; however, no epidemic problems were encountered as in the previous year's two rearings.

The fish were released 20-21 November. The number released, adjusted for tag recognition percentages provided by CDFG, was 11,223 at an average weight of 75 g. The total number released was 12 percent higher. The adjusted figure for the control group was 21,730. The adjustment for tag recognition purposes is an estimate based on the size of fish, the experience of the tagging crew, and other factors which might affect tag retention and recognition of the adipose-fin clip.

Results and Discussion

Growth

The average weight of salmon in all groups increased exponentially with time during the rearing period. Growth curves fit to average weight at delivery and release for all nine groups of salmon are presented in Figure 4. The mean weight of each rearing group (except 3, 4 and 5) doubled during each 30- to 32-day period they were in the pens.

Group 3 cohos, yearling fish delivered in January 1976, grew more slowly than any other group. Their mean size was large at delivery and the size range was extreme. Both factors, together with cool winter water temperatures, probably accounted for the slow growth.

Somewhat slower growth was noted in Groups 4 and 5 than in the remaining six groups. For Group 4, the likely cause was cool water; for Group 5 the range of size at delivery was so extreme that the growth curve based on mean size was of little significance.

Tagging Mortality, Tag Shedding, and Tag Recognition

The returning coho salmon from the 1975 and 1976 releases provided an opportunity to estimate the combined tag shedding and tagging mortality of these Carlin-tagged fish during their time spent at sea. The releases consisted of the 1975 fall and 1976 spring Tiburon releases, and a 1975 UCSG release which had been held at Tiburon for a week before transfer to and rearing in Tomales Bay. The Tomales Bay salmon apparently imprinted to the Tiburon site, as returns for this group were recorded only at Tiburon.

The estimation of tagging mortality and/or tag shedding involved comparing numbers of tagged and untagged salmon released with the numbers of tagged and untagged returning salmon captured in a gill net set at the pen site in 1976. All returning cohos were assumed to be returns from the 1975 and 1976 releases rather than wild stock, as wild cohos were not normally found in the San Francisco Bay-Delta system. None of the adipose-fin-clipped cohos released in 1974 were caught in the gill net. The gill net was assumed to be an unbiased sampling gear with respect to untagged and tagged fish. A *t*-test was used to determine if the length of tagged and untagged fish had the same mean. Mean length was equal at the 0.01 significance level so the assumption seemed justified.

Given these circumstances, the percent tagging mortality and/or tag shedding while at liberty is:

$$M = \left[1 - \left(\frac{C_t}{R_t} \right) \div \left(\frac{C_u}{R_u} \right) \right] \times 100,$$

where M = tagging mortality and/or tag shedding,
C_t = number of tagged salmon recaptured by gill net,
R_t = number of tagged salmon released,
C_u = number of untagged salmon recaptured by gill net, and
R_u = number of untagged salmon released.

It was not possible to distinguish between tag shedding and tagging mortality, as only tagged vs. untagged fish were discernible after return to the gill net. The tagging mortality/tag shedding rates in these releases were very high. Only 20 tagged salmon were among the 159 caught in the gill net. Of the total of 43,118 salmon released, 16,552 were tagged. This would indicate a tagging mortality and/or tag shedding rate of 77 percent.

It follows that, in the absence of such tagging mortality/tag shedding, 4.3 times as many tagged fish would have been recaptured. This adjustment was used in estimating return rates (Table 2). An assumption has been made that the tagging mortality/tag shedding rates were the same for all groups of Carlin-tagged fish and has been used in estimating the percentage of tag recoveries for all groups released with Carlin tags.

In the case of nose-tagged fish, recoveries from the sport and commercial ocean catch are made by samplers at each port where the fish are landed. Total nose-tagged fish returns are then estimated by the CDFG by dividing the number of actual recoveries by the percentage of the landings sampled. This calculation estimates the number of nose tags that would be recovered if all the landings were censused.

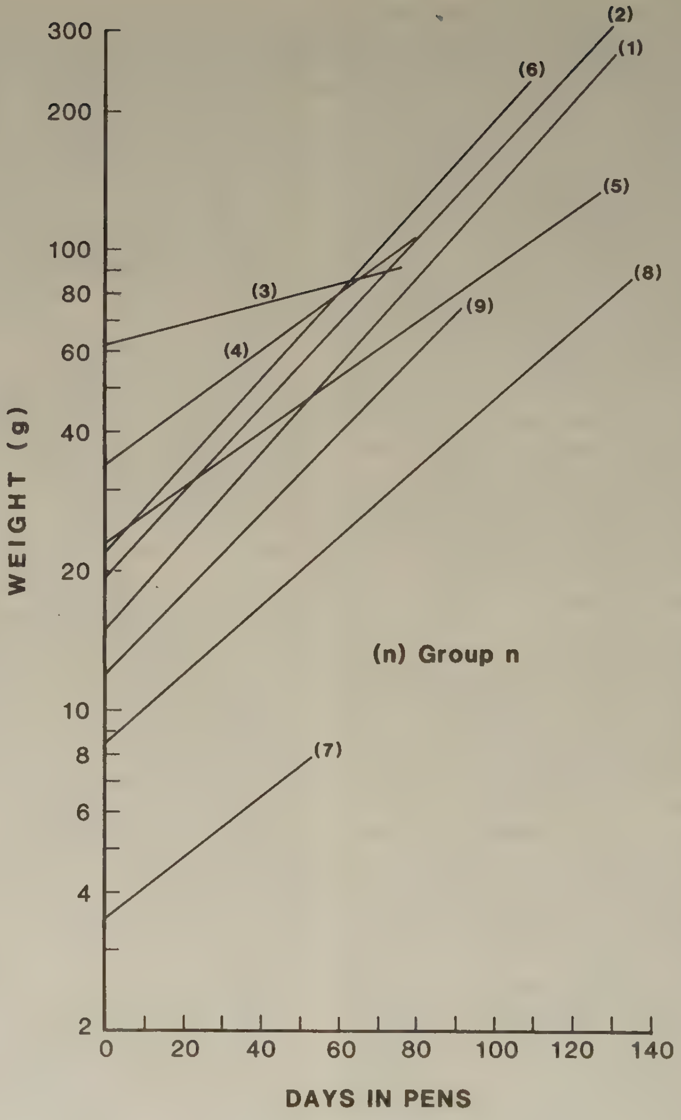

Figure 4.—Growth curves for pen-reared salmon by group.

Our freeze-branding trial produced no returns. It can be concluded that the marks faded, because Carlin-tagged fish that were recaptured from Group 6 showed no evidence of having been freeze-branded.

Tag Returns

Tag returns are important because they measure the contribution of each group to the fishery. Several factors in this study make it difficult to analyze the tag return information and therefore to draw conclusions from it. There was a high degree of variability in the rearing experience from year to year. Changes in species, brood stock, hatchery, date, size, and uniformity of size at delivery were usually dictated by factors that were beyond the control of the experimenters. Varied environmental conditions, such as the drought in 1975 and 1976, not only affected rearing conditions but also caused some regulatory changes (season and size) that may have influenced tag return rates. It is also likely that the adipose fin clip identifying nose-tagged fish escaped observation in some groups more than others. For example, many cohos from Group 1 were caught by sportfishermen fishing along the shoreline of the Bay, where their catches were not censused. Group 1 returns therefore are probably underestimated.

Table 3.—Nose-tag retuns from Group 9.

	Subgroup				
	Control		Pen-reared		
Years recovered	Number recovered	Percent of release (21,730)	Number recovered	Percent of release (11,223)	Percent of delivery (67,900)
1980	0	0	14	0.1	0.0
1981	503	2.3	1,243	11.1	1.8
1982	69	0.3	178	1.6	0.3
Total	572	2.6	1,435	12.8	2.1

Because a minimum mesh size of 22 mm was found to be necessary to assure adequate circulation and prevent the attendant problems of fouling and reduction of dissolved oxygen, many fish escaped soon after delivery and throughout the rearing period. Unfortunately this problem occurred in all the batches of nose-tagged fish that were received. To whatever extent such fish survived after their escape, the return rates are overestimated because the pool of tagged fish from which recoveries were drawn would have been larger than the number used to calculate the percentage or rate of recoveries. The groups most affected were 8 and 9. There also was a mass escape from Group 7, but it is unlikely that many of these pre-smolt fish survived[4].

As would be expected from the preceding discussion, the tag return rates varied greatly from group to group. Nonetheless, certain trends appear and we believe that despite the various dissimilarities and uncertainties from year to year, certain conclusions become apparent from a subjective analysis of the tag returns.

The best return rate was from Group 4, the first batch of chinooks reared. As stated, this group was healthy throughout the rearing period. Although more than half of the fish escaped, those fish had not been tagged and would not affect the return rate calculation. The mean weight at delivery was the second largest of all the groups, and the size variation was small. Also, these fish were reared in the autumn when the water temperature was cool. As noted, this was one of the groups that grew somewhat more slowly than most others. Whatever the reason, the tag return rate of 23.5 percent (adjusted) was four times as good as from any other of the externally tagged groups.

The worst return rate for external tags was from Group 5, the first group of 1977 cohos. Only two tags were recovered, for an adjusted rate of 0.4 percent. Apparently the extreme size range (10-199 g) and poor health at delivery were contributing factors.

The next lowest return rate for Carlin-tagged fish was from the second batch of 1977 cohos, Group 6. This group suffered a high initial mortality—about one-third—and the fish were much handled, having undergone freeze-branding as well as Carlin-tagging.

The Group 7 experiment, which was fraught with problems from start to finish, produced the lowest return rate of nose-tagged fish. The critical factor in this group probably was the small size of the fish at delivery and release.

Earlier in this section we suggested that nose-tag return rates for Groups 8 and 9 are overestimated. The release of Carlin-tagged fish as well as nose-tagged fish in Group 8 provides an opportunity to gauge the magnitude of the overestimate by comparing the return rates for the two types of tags. The 13.3 percent return rate estimate for the nose tags is about 2.25 times as high as the 5.9 percent return estimate for the Carlin tags. This "overestimate factor" is subject to some degree of uncertainty because the Carlin-tagged and nose-tagged fish had slightly different histories. Nonetheless, it is probably realistic to assume that at least as many nose-tagged fish escaped and survived as were released and counted at the end of the rearing period.

The Group 9 experiment compared the return rate from pen-reared fish with those from a control group released at the pen site at the beginning of the rearing period. Table 3 summarizes the tag recovery data from Group 9. The return rate for the control subgroup was 2.6 percent. The return rate for the pen-reared subgroup is given first as a percentage of the fish that were counted out of the pen after the rearing period. The 12.8 percent figure neglects the more than 55,000 fish (adjusted for tag recognition) that were not accounted for in the release, most of which escaped. The second tag recovery rate is given as a percentage of all the fish that were delivered to the pens for rearing. Even though only one-sixth of the fish that were delivered for pen rearing were actually pen-reared, the 2.1 percent return in this comparison suggests that pen rearing was not advantageous.

Cost Effectiveness of Pen Rearing

One problem with the preceding analysis of tag returns from Group 9 deliveries of chinook salmon is that the

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[4] Fred Meyer, California Department of Fish and Game, Region 2, Rancho Cordova, Calif. Personal commun.

Table 4.—Annual pen-rearing costs for 40,000 fish for 3 months; labor = $50/worker-day.

Item	Cost (dollars)	
	Materials	Labor
Nets and pens		
amortized at 12% over 10 years	$2,650	
maintenance and repair	400	$1,800
Medications	800	300
Feed	3,000	4,500
Miscellaneous supplies	1,700	
Subtotal	$8,550	$6,600
Grand total, materials and labor	$15,150	

experience with Group 9 was not a best-case episode. The fact that a 23.5 percent return of tagged fish was achieved once suggests that under a certain set of circumstances pen rearing might be a cost-effective management technique for augmenting ocean harvest.

Critical to determining the benefits of pen rearing is the cost involved—specifically, the cost in producing the incremental increase in returns that can be attributed to the pen rearing. To deal with this question, it is necessary first to accept a return rate that might be expected from fish released directly into San Francisco Bay, as was the control portion of Group 9. Recent CDFG studies have led to their adopting a policy of releasing chinook smolts (45/pound or 10 g/fish), instead of yearlings, directly into San Francisco Bay. Return rates have been as good or better (up to 4 percent) than for yearlings and cost per fish is lower[4].

If we assume a cost of $0.06/fish to rear salmon to 45 fish/pound (an approximation using data from McCormack et al., 1984, which does not include an amortization of capital costs) and a 4 percent return, then each fish caught represents an operational investment of $1.50.

The annual costs of pen rearing 40,000 fish for 3 months are shown in Table 4. Capital expenditures are amortized over 10 years at 12 percent interest, and labor costs valued at $50 per worker-day. If we assume that good pen-rearing techniques will bring about an ocean harvest of 25 percent of those fish released, then the cost of adding 10,000 fish to the catch would be $15,150, or roughly $1.50 for each fish. This cost does not include fixed costs, lease fees, management salary, or the cost of hatching and rearing the 40,000 fish to the size at which they would be introduced into the pens.

The objective of establishing a sport fishery for coho inside the Bay was best met by Group 1. Sufficient numbers returned to and remained in the vicinity of the rearing site that a fairly extensive fishing effort developed. The local fishery was less evident in subsequent rearings, possibly because we were no longer able to obtain fish from the Noyo River brood stock. Further testing with Noyo River fish would be required to determine if a sport fishery for coho could be consistently established inside San Francisco Bay.

Summary

Our successful experience with the Group 4 chinooks demonstrated that pen rearing is, indeed, possible in San Francisco Bay, and that chinook salmon have excellent potential for the various forms of net-pen salmon ranching. On the other hand, we know that the hatchery production cost of 40,000 fish that can be either directly released or released after pen rearing is roughly $2,400. If we assume that the respective return rates for the two procedures would be 4 and 25 percent, then we can choose between getting 1,600 returns at a cost of $2,400, or an additional 8,400 returns for an additional cost of $15,050. The additional cost per additional return then, is about $1.80 for each fish. To the extent that our assumed return rates are valid, this project did not demonstrate that pen rearing would be a cost-effective management technique for adding to the ocean harvest in California. However, cost efficiency probably would improve if the project were scaled up.

Acknowledgments

Members of the San Francisco Tyee Club participated in pen construction and maintenance, tagging, and feeding. We are especially grateful to Jean Lestanguet for his efforts on behalf of the Tyee Club. Tag rewards were paid from Tyee's treasury. Seventy different people spent long hours at the tedious task of tagging and we thank them all. We wish also to thank Sus Kato of the Tiburon Laboratory for his guidance and manuscript review and reviewers Earl Prentice of the NMFS and Fred Meyer of the CDFG. Valuable contributions were also made by CDFG hatchery personnel and State Fish Disease Laboratory staff.

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A history of California rockfish fisheries

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Abstract

Rockfish have been caught off California since prehistoric times. While 60 species are recorded in California waters, less than 20 species make significant contributions to landings by the diverse gears that are used in the fisheries. This paper reviews dynamics in the size and composition of the fishing fleets and landings. Recent events in the fisheries are compared with the history, and important management and research problems of the present are discussed.

History of Landings

Californians have captured rockfish for centuries. California Indians consumed rockfish in prehistoric times (Fitch 1972). Rockfish had attained commercial importance in California by 1875 (Phillips 1957). By the turn of the century, annual landings had reached about 750 mt and there were about 1,500,000 people in the state. Now, with 25,000,000 people, landings of rockfish have increased to 20,000 mt, a 60% gain in landings per capita. The California Department of Fish and Game began compiling fish receipt data in 1916 (Heimann and Carlisle 1970; Figure 1). These data include most landings, but some small landings do not enter normal market channels and are not included.

The landings were fairly stable, generally between 2,000 and 4,000 mt, until the Second World War first interfered with the fishery and then created a large demand. Until 1943, most rockfish were caught by hook-and-line gear; only 5% were landed by trawlers. In late 1943, a boat moved from Astoria, Oregon, to Eureka and used a high-rise trawl called a "balloon trawl" (Phillips 1949). The balloon trawl was very

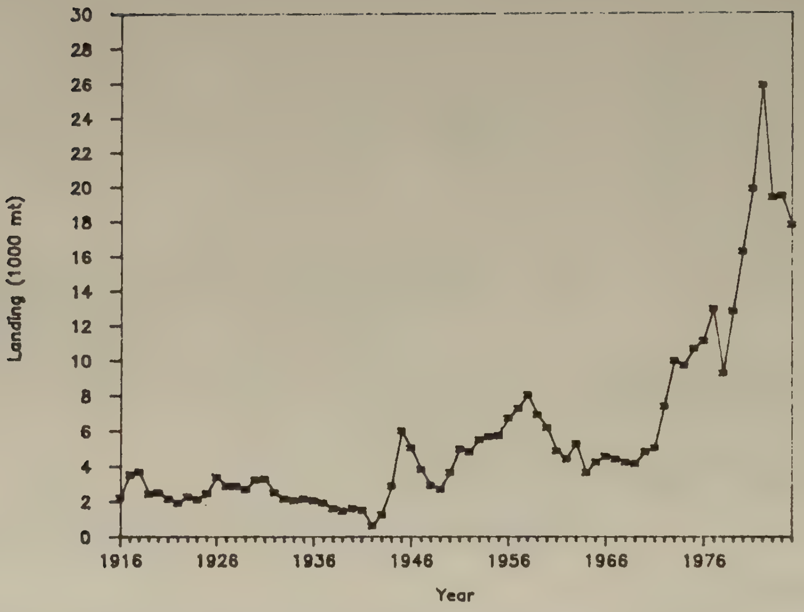

Figure 1. California commercial landings of rockfish, 1916–1985.
Source: 1916–1968 (Heimann and Carlisle 1970),
1969–1970 (Bell 1971),
1971 (Oliphant et al. 1973),
1972–1974 (McAllister 1975, 1976),
1975 (Pinkas 1977),
1976 (Oliphant 1979),
1977–1980 (Frank Henry, personal communication), and
1981–1985 (PacFIN).

effective in capturing rockfish. Use of the balloon trawl spread rapidly and trawl-caught rockfish have dominated the landings since 1944. A peak occurred in landings in 1945 because of the demand from army camps on the West Coast. Landings declined at the end of the war when the camps were phased out.

I did not find explanations for fluctuations in landings between 1950 and 1970. During the past 15 years, landings have increased considerably as the result of better market demand, net design, acoustics, and navigation. Landings peaked in 1982. In that year, many boats from Oregon and Washington fished in northern and central California. These vessels made large landings of widow rockfish (*Sebastes entomelas*) as well as other species of rockfish. In addition to the expanded trawl effort in the 1980's, gill-net vessels also have increased effort.

Since 1983, widow rockfish landings and, to some degree, landings of other species have been constrained by Pacific Fishery Management Council regulations.

The hook-and-line fishery in the early days was fairly primitive. Most trips lasted less than a day and often the crew size was one. Most fishing took place close to port and in water less than 100 fathoms (Scofield 1947). Landings were dominated by black rockfish (*S. melanops*) in northern California, bocaccio (*S. paucispinis*) and chilipepper (*S. goodei*) in central California, and vermilion rockfish (*S. miniatus*) in southern California. After the advent of the balloon trawl, canary rockfish (*S. pinniger*) replaced black rockfish in northern California and bocaccio and chilipepper replaced vermilion rockfish in parts of southern California. Catches of widow rockfish were minor before 1979 when vessels with midwater trawls began targeting on them. In very recent years, bank rockfish (*S. rufus*) have become more important in landings.

Trawl fishery

It is not very meaningful to discuss solely the California trawl fleet, because many vessels fish in more than one state during the year. The fleet is very dynamic. Of the 600 trawlers that participated in the California, Oregon, and Washington fishery for groundfish between 1981 and 1984, only 400 participated in the 1984 fishery. Of the 200 that didn't, records are incomplete for about half (E. Ueber, personal communication). We do know that about 50 sank or burned, 30 fished in other areas or for other groups of fish, and 30 didn't operate because of bankruptcy or other problems.

Most trawl-caught rockfish enter the fresh fish market as fillets. In recent years, widow rockfish, bocaccio, chilipepper, and bank rockfish have dominated the trawl landings. The ex-vessel price of most trawl-caught rockfish is $0.275/lb. The trawl landings of rockfish in California are worth about $10,000,000.

Gill-net fishery

Another important gear for rockfish in southern and central California is the gill net. This gear is prohibited in northern California. Landings by this gear are not as dominated by widow rockfish, bocaccio, and chilipepper as trawl landings are. Yellowtail rockfish (S. flavidus) and blue rockfish (S. mystinus) are also important.

In 1985, almost 900 vessels were licensed to use gill nets (E. Ueber, personal communication). While I do not have accurate data, probably several hundred gill-net vessels landed rockfish in California.

Our data for California gill-net landings are incomplete, but the catch of rockfish was more than 2,700 mt in 1985. Gillnetted fish tend to be worth more than trawl-caught fish. I estimate that 1985 landings were worth several million dollars to the fishermen. While some gillnetted rockfish are filleted, many enter the market as whole or dressed fish.

A number of problems are associated with the gill-net fishery in California. Besides the usual gear conflicts, there are major incidental kills of seabirds and marine mammals. Because of the problems, there is considerable public support to either ban the gear altogether or severely restrict it.

Hook-and-line fishery

Rockfish are still commercially caught by hook-and-line fishermen in California. While this fishery captures the same species as the other gears, there is a greater tendency to fish for specialized markets such as the Chinese restaurant trade. The brown rockfish (S. auriculatus) and several closely related species are preferred for this market. Fishermen receive as much as $3.00/lb for fish in good condition. Sometimes the fish are kept alive until just before cooking.

I don't have a firm estimate of the number of hook-and-line vessels fishing for rockfish in California. It is approximately 300. 1985 landings were about 1,000 mt. I estimate that these landings were worth 1 to 2 million dollars. Most hook-and-line caught rockfish enter the market as whole or dressed fish.

Recreational fishery

Rockfish are very important for recreational fisheries. Besides being good eating, rockfish can be as large as 28 lbs (such as the cowcod, S. levis), can be very colorful (such as the starry rockfish, S. constellatus), and can be very attractive when viewed underwater (such as the treefish, S. serriceps). While catches are usually dominated by one or two species, we have sampled more than 12 species on a single party-boat trip. The variety is appealing to some anglers.

While the California recreational fishery probably is worth more than commercial fisheries of most nations, it is not very well documented. This is because it is difficult to adequately sample recreational landings. Statistics have been collected from the party-boat fishery through a logbook system since 1936 (Collyer 1949, Young 1969). Since 1981, the entire fishery has been sampled by a phone interview and field sampling program (U.S. Department of Commerce 1986).

The party-boat fishery is concentrated in southern California. Prior to the 1950's, rockfish did not support a major targeted fishery in southern California. Anglers preferred the then abundant barracuda (*Sphyraena argentea*). Barracuda numbers declined and rockfish became very important in the party-boat fishery. The party-boat fishery for rockfish is still minor in northern California.

In 1985, recreational anglers landed almost 8,000,000 rockfish in California (U.S. Department of Commerce 1986). The fish weighed about 4,000 mt. Rockfish comprised almost 1/3 of all recreational fish landed in the state and are the most important group of species. Forty-six species of rockfish were sampled from recreational catches in 1984. However, three species--blue rockfish, black rockfish, and yellowtail rockfish--represent about 30% of the landings. Boat anglers make more than 90% of the landings. Landings from party boats and private boats are about equal.

Economists have yet to agree on how to determine the value of a recreational fishery. One method is to appraise all costs associated with fishing trips. Using this approach, economists estimated that the California recreational fishery for all species is worth about a billion dollars (D. Huppert, personal communication). This is not equivalent to the commercial fisheries values, because there are many factors included in the recreational value not included in the ex-vessel value of commercially landed fish. Still it appears that the recreational value significantly exceeds the commercial value. Agencies recognize this when making management decisions.

Status of fishery

Most stocks of traditional rockfish species in California are at or below the MSY level. Some, such as bocaccio, may be overfished. Present regulations consist of a quota on widow rockfish, 40,000-lb trip limits on commercially caught fish, and a 15-fish bag limit for recreational fish. There are also various gear and area restrictions. The objective of many of the area regulations is to reduce gear conflicts, particularly between recreational and commercial fishermen.

While most of the traditional species are fully utilized, two appear not to be. Recent analysis indicates there is some room for expansion in landings in chilipepper. In addition, bank rockfish landings have increased in recent years. They occupy a habitat that had only been lightly fished previously.

There are two other abundant, lightly exploited species. The splitnose rockfish (*S. diploproa*) is quite abundant. However, it is a very long-lived species and, while the fishery probably could be expanded some, care is needed in such an expansion because the species could easily become overfished. It is a marginal commercial fish because it produces low fillet yields and is fairly small. Shortbelly rockfish (*S. jordani*) is very abundant and short-lived. The species probably could support a fishery about the size of the other species combined.

However, it is quite small (maximum size about 30 cm) and must be processed rapidly.

Species targeted by recreational fisheries in southern and central California appear to be fully utilized. Some of the expansion of the recreational fishery has come at the expense of the commercial fishery. Several nearshore species--e.g., black, blue, and yellowtail rockfish--appear to be lightly fished in northern California. Recreational fishing in this area is limited because of the distance from population centers.

Discussion

During historical times the commercial fishery has passed through several phases (Figure 1). Between 1916 and 1947, landings were generally between 2,000 and 4,000 mt. During the Second World War, fishing techniques and markets improved and landings increased to between 4,000 and 8,000 mt until 1971. Since then, techniques and markets have again improved and landings are now about 20,000 mt. The status of exploited species indicates that landings will be between 10,000 and 30,000 mt until other species are harvested. If an increase occurs, it would be a repeat of history. The previous major increases involved changes in the relative importance of species. A future major increase also is likely to involve changes in species composition of landings. Shortbelly and splitnose rockfish are likely to contribute to increased landings. As in the past, improved market conditions are a prerequisite to increased utilization of these two species.

History may also be repeated in the recreational fishery. Significant expansion of recreational landings of rockfish in southern and central California is not likely to occur without reduction of commercial landings.

Management and researchers involved with California rockfish fisheries face several major problems including conflicts between recreational and commercial fisheries. I have already mentioned the gill-net problem. There also appears to be some overcapitalization. The industry, researchers, and managers have been discussing various forms of limited access management, but implementation of such management appears to be years, if not decades, off. Fluctuations in year-class strength cause the fishery to be somewhat unpredictable. Research aimed at this problem is discussed in another paper (Kendall and Lenarz 1987). Researchers are also attempting to develop optimal management strategies that account for the multispecies aspects of the fishery. Finally, monitoring the fishery is quite expensive. We are working on procedures to make sampling more efficient.

Acknowledgments

I gained much of the information contained in this paper from conversations with my colleagues. Frank Henry and Tom Jow of the California Department of Fish and Game, Menlo Park, and Sus Kato and Ed Ueber of NMFS, Tiburon, are particularly knowledgeable of California fisheries.

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NOTES

COMPARISON OF VISCERAL FAT AND GONADAL FAT VOLUMES OF YELLOWTAIL ROCKFISH, *SEBASTES FLAVIDUS*, DURING A NORMAL YEAR AND A YEAR OF EL NIÑO CONDITIONS

One of the severest El Niño events of the century occurred off California during late 1982 and most of 1983 (Rasmusson 1984). Associated with the warm water and lack of upwelling were impressions by many fishermen and biologists that macroplanktonic organisms were at low densities and that fish were thinner than normal. A semiquantitative sampling program off of San Francisco indicated that euphausiids, a major component of the macroplankton, were considerably less common in 1983 than in either 1982 or 1984 (Smith[1]).

Yellowtail rockfish are abundant off northern California and are an important component of recreational and commercial catches in some areas. The species feeds mostly on macroplanktonic organisms such as euphausiids, salps, and small fish (Phillips 1964; Pereyra et al. 1969; Lorz et al. 1983). Annual cycles of visceral fat volume and gonad volume are documented in Guillemot (1982) and Guillemot et al. (1985). The studies showed that visceral fat volume in both sexes of yellowtail rockfish is at a maximum during fall. The viviparous species (Boehlert and Yoklavich 1984) mates in early fall (September) and releases larvae during winter (January-March) (Wyllie Echeverria[2]). Guillemot (1982) and Guillemot et al. (1985) showed that male gonad volumes peak in fall and female gonad volumes peak in winter.

The purpose of this study is to determine possible effects of El Niño conditions by comparing visceral fat and gonad volumes during 1983, a year of El Niño conditions, with data collected during 1980, a normal year (Guillemot 1982).

Methods and Materials

Guillemot (1982) and Guillemot et al. (1985) utilized data collected throughout the year. The 1983 data were collected only on 21 September, the approximate sexual activity peak for males, and 20 December, which slightly precedes the peak time of larval release for females. Only 1980 data collected within 20 d of the two 1983 collection dates and samples collected from central California, between Bodega Bay and Half Moon Bay, were used in this study. In 1983 all specimens were collected from landings made at Bodega Bay.

Specimens were sexed, measured to the nearest millimeter for total length, and viscera were removed and preserved in 10% buffered Formalin[3] in the field following the procedures of Guillemot et al. (1985). After about 90 d of storage, visceral fat and gonad volumes were measured to the nearest milliliter by water displacement. Visceral fat of some fish had dissolved to form a floating liquid. The volume of this liquid was measured and added to the total fat volume. Data from males larger than 379 mm, when 90% are mature, and from females larger than 380 mm, when 85% are mature, were used (Wyllie Echeverria fn. 2).

As in Guillemot (1982) and Guillemot et al. (1985) we used the following power equation to describe the relationship between fat or gonad volume and length:

$$Y = \alpha X^{\beta}$$

where Y = fat or gonad volume, and
X = total length.

The parameters were estimated by first transforming the variables to natural logarithms and then using standard least squares linear regression techniques. Analysis of covariance was used to determine if separate lines for the two years significantly reduced the variance from a common line (Kleinbaum and Kupper 1978). This is a fairly robust test in that if there is not a significant linear relationship between the two variables for one or both time periods, the test is nearly as powerful for comparing the two means as an analysis of variance.

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[1] Smith, S. Unpublished data. Tiburon Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[2] Wyllie Echeverria, T. 1983. Reproductive seasonality and maturity of the rockfishes (Scorpaenidae; *Sebastes*) off central California. Unpubl. manuscr., 66 p. Southwest Fisheries Center, Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

The regression lines for the male fat volume for the two years intersect and are not significantly different (Table 1). The results of the analysis of covariance for fat volume of females are highly significant (Table 1). Females had significantly higher fat volumes in 1980 for both months (Fig. 1).

The comparisons of gonad volumes produced highly significant results in December for both sexes, and for females in September (Table 2). Female gonad volumes were higher in 1980 during December and lines intersected in September (Fig. 2). Male gonad volumes were significantly higher in December 1983 than in December 1980.

TABLE 1.—Results of analysis of covariance of fat volumes of yellowtail rockfish regressed on length. Observations were transformed to natural logarithms for the analysis.

		1980			1983			
Sex	Month	Sample size	Intercept	Slope	Sample size	Intercept	Slope	*F*
Male	September	20	−9.884	2.011	38	22.272	−3.355	2.753
Male	December	17	7.198	−0.978	35	35.402	−5.693	2.571
Female	September	25	−9.327	2.003	46	5.443	−0.449	11.917**
Female	December	19	21.813	−3.262	50	1.609	−0.058	5.889**

**Significant at 99% level of confidence.

The seasonality of gonad development was similar in the two years, but appeared to be delayed in 1983. Males were 50% maturing and 50% resting in September 1980, and 100% resting during December. In 1983 males were 100% maturing during September, and 8% maturing and 92% resting during December. Females were 35% maturing and 65% resting in September 1980, and 83% maturing and 17% resting in December. In 1983 females were 100% maturing during September, and 97% maturing and 2% resting during December. Data on season or parturition for 1981-84 (Table 3) indicate that parturition was delayed in 1983 and 1984 compared with 1981 and 1982.

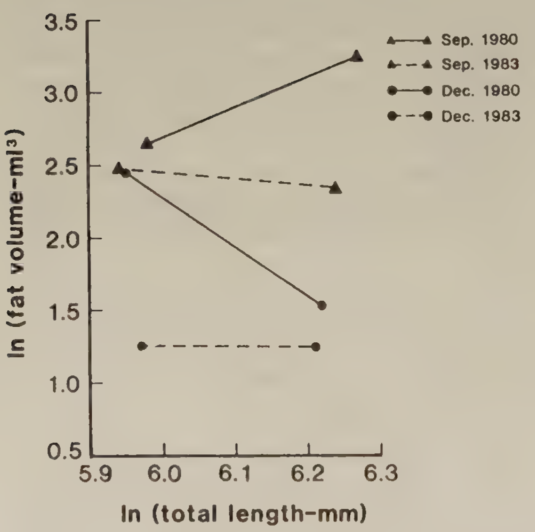

FIGURE 1.—Relationships between ln (visceral fat volume) and ln (total length) for female yellowtail rockfish in 1980 and 1983.

Discussion

The results tend to agree with expectations. Female fat volumes were lower in 1983 than in 1980, which is in agreement with the impressions of fishermen and the expectation that El Niño would produce relatively poor feeding conditions and consequently result in thin fish.

TABLE 2.—Results of analysis of covariance of gonad volumes of yellowtail rockfish regressed on length. Observations were transformed to natural logarithms for the analysis.

		1980			1983			
Sex	Month	Sample size	Intercept	Slope	Sample size	Intercept	Slope	*F*
Male	September	20	−35.589	6.161	38	−25.205	4.450	0.274
Male	December	17	−50.003	8.290	35	−11.037	1.962	8.170**
Female	September	25	−54.09	9.171	46	−31.019	5.406	3.404*
Female	December	19	−56.674	9.855	50	−45.723	7.908	12.224**

**Significant at 99% level of confidence.
*Significant at 95% level of confidence.

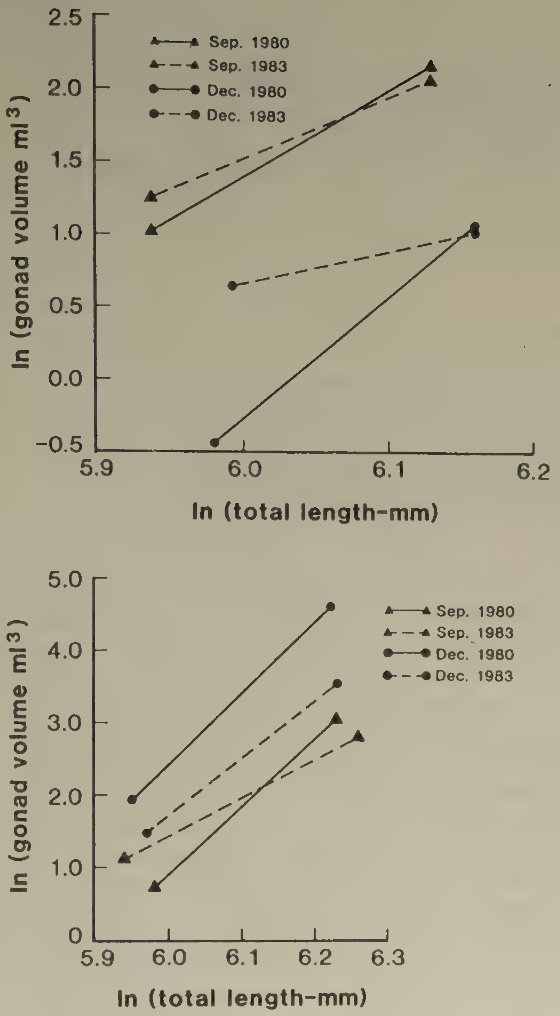

FIGURE 2.—Relationships between ln (gonad volume) and ln (total length) for yellowtail rockfish in 1980 and 1983. (Top) males; (bottom) females.

TABLE 3.—Percent of yellowtail rockfish females with eyed-larvae observed in samples collected in central and northern California, 1981-1984.

Year	January	February	March	April	May	June
1981	5	0	0	0	0	0
1982	0	15	0	0	0	0
1983	0	18	16	6	0	4
1984	3	10	15	0	0	0

The lower ovary volumes in 1983 than 1980 could have been related to either delayed parturition and/or lower reproductive effort. Wootton (1979) described relationships between feeding conditions and fish fecundity. The significantly higher gonad volumes for males in December 1983 compared with 1980 were not expected. December is later than the normal period of sexual activity for males, but the unexpected gonad volume results may be caused by delayed mating. The gonad stage data indicated that male sexual activity was later in 1983 than in 1980.

While fish condition and reproduction were different in 1983 than in the preceding non-El Niño years, the documentation of such differences for marine fish is uncommon. The season of parturition of yellowtail rockfish is more variable than we realized when the study was designed and the data on fish condition and gonad volume should have been collected over a wider period of time. The results of our study indicate that the assumption of constant adult fish condition and reproductive effort that is usually made in models of the population dynamics of fish is questionable.

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MODELING LIFE-STAGE-SPECIFIC INSTANTANEOUS MORTALITY RATES, AN APPLICATION TO NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, EGGS AND LARVAE

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ABSTRACT

Life-stage-specific instantaneous mortality rates (IMRs) are often estimated individually for each life stage of an organism using regression analysis. A single estimation procedure for all life stages may be preferable because it would increase the overall precision of the IMRs and also provide a more realistic mortality model. Two such procedures were developed in this paper. One is single-equation model where regression estimates of all IMRs are obtained by fitting a single survivorship function to the entire data set. The other is the maximum likelihood estimator. These models were compared using northern anchovy egg and larval data. The survivorship functions of each were, respectively, exponential and Pareto functions.

The mortality of marine fish can be described by its survival probability $S(t) = P(T > t) = \exp[-\int_0^t \lambda(u)du]$, where T is the age of the fish and $\lambda(t)$ is the instantaneous mortality rate (IMR) at age t. During their early life history, pelagic marine fishes pass through a series of life stages: eggs, yolk-sac larval, feeding pelagic larval, juvenile and adult stages. The IMR $\lambda(t)$ could be different for some life stages. Therefore, for I life stages, there may be G distinctive IMRs where $G \leqslant I$. The IMR $\lambda(t)$ is then a piecewise function (Gross and Clark 1975, p. 20-21; Johnson and Kotz 1976, p. 272-273)

$$\lambda(t) = \begin{cases} \lambda_1(t) & 0 \leqslant t \leqslant u_1 \\ \lambda_2(t) & u_1 \leqslant t \leqslant u_2 \\ \cdot & \cdot \\ \cdot & \cdot \\ \lambda_g(t) & u_{g-1} \leqslant t \leqslant u_g \\ \cdot & \cdot \\ \cdot & \cdot \\ \lambda_G(t) & u_{G-1} \leqslant t \leqslant u_G \end{cases}$$

where u_g is the maximum age of mortality stanza g. $\lambda_g(t) \neq \lambda_{g'}(t)$ for $g \neq g'$. For example, $\lambda_1(t)$ may be the IMR for egg and yolk-sac larval stages, even though each is a different life stage, and $\lambda_2(t)$ the IMR for feeding larvae. As a result, the conditional survival probability, $S_g(t) = P(T > t | T \geqslant u_{g-1})$ corresponding to $\lambda_g(t)$, will also be different from $S_{g'}(t)$ and the survival probability $S(t) = (P\,T > t)$ will be

$$S(t) = \begin{cases} S_1(t) & 0 \leqslant t \leqslant u_1 \\ S_1(u_1)S_2(t) & u_1 \leqslant t \leqslant u_2 \\ \cdot & \cdot \\ \cdot & \cdot \\ \cdot & \cdot \\ \prod_{d=1}^{G-1} S_d(u_d)S_G(t) & u_{G-1} \leqslant t \leqslant u_G \end{cases}$$

The common method for estimating $\lambda_g(t)$'s for marine fishes has been to fit $S_g(t)$ to sample age data separately for each life stage or to assume one common $\lambda(t)$ for all life stages and to fit one $S(t)$ to sample data of all life stages (Hewitt and Brewer 1983). For northern anchovy, *Engraulis mordax*, eggs and larvae <20 d old, the IMR $\lambda(t)$ for eggs and yolk-sac larvae is different from that of the feeding larvae (Lo 1985):

$$\lambda(t) = \begin{cases} \lambda_1(t) = \alpha & 0 < t \leqslant u_1 \\ \lambda_2(t) = \dfrac{\beta}{t} & u_1 \leqslant t \leqslant 20 \end{cases} \qquad (1)$$

where u_1 is either the hatching time ($t_h \sim 3$ d) or the age of yolk-sac larvae ($t_{ys} \sim 4.5$ d) with the first feeding as the critical period after which mortality decreased. Either t_h or t_{ys} has been used in various models under different assumptions. If morphological differences cause the changes in mortality rates, t_h is a reasonable separation point between

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egg and larval stages. However, predation, the major cause of mortality in the embryonic period, may be similar for eggs and yolk-sac larvae (Hunter[2]). If this is true, then the end of the yolk-sac stage is a reasonable separation point for the mortality stanza.

The conditional survival probability corresponding to IMR in Equation (1) is

$$S_1(t) = e^{-\alpha t} \qquad t \leqslant u_1 \qquad (2a)$$

and

$$S_2(t) = \left(\frac{t}{u_1}\right)^{-\beta} \qquad u_1 \leqslant t \leqslant 20 \qquad (2b)$$

To assess $S_g(t)$ for $g = 1,2$ in Equation (2), anchovy egg and larval data were first divided into K age groups. The mortality curves (Equation (3)) were fitted to the sample mean counts $(\bar{y}_i)$ and mean age (t_i) $i = 1,\ldots,K$:

$$E(\bar{y}_i) = \begin{cases} \theta_0\, S_1[t_i;\, \lambda_1(t)] & t_i \leqslant u_1 \\ \theta_{u_1}\, S_2[t_i;\, \lambda_2(t)] & u_1 \leqslant t_i \leqslant 20 \end{cases} \qquad (3)$$

where θ_t is the expected number of fish at age t. Using separate equations like Equation (3) is unsatisfactory for some applications because separate mortality curves may produce discontinuities at transitions between mortality stanzas (or life stages). The purpose of this paper is to obtain a regression estimator and a maximum likelihood estimator (MLE) of the IMRs $(\lambda(t))$. The regression estimator was based upon a single mortality curve for all early life stages of anchovy, and the MLE was based upon a truncated exponential (Equation (2a)) and Pareto (Equation (2b)) likelihood function of time to death (Lo 1985).

In section on Data, I describe the method of anchovy egg and larval data collection and standardization procedures. The standardization procedures are necessary because the gear and sample sizes used to collect eggs differ from those used to collect larvae. In section on Multi-Equation Model, the current estimation procedures for constructing mortality functions for different life stages are presented. In these procedures separate mortality functions are fitted to the data set for each life stage. In the next two sections, I develop two estimation procedures for the IMRs of different life stages from a single analysis: a single mortality function is constructed which is based on the IMRs of different life stages, and the maximum likelihood estimators of life-stage specific IMRs are described. The MLEs of anchovy eggs and larvae (<20 d) are obtained. The results and the comparisons of various models based on anchovy egg and larval data are given in the last two sections.

DATA

The standardized abundance of anchovy eggs and larvae taken in routine biomass surveys was used to elevate different estimation procedures for mortality rates (Smith 1972; Parker 1980). The variables used in the standardization procedures were extrusion through the net, avoidance of the net mouth, and the variation of the water volume filtered per unit depth (Zweifel and Smith 1981).

The northern anchovy spawning area lies off central and southern California and Baja California. The sampling area was divided into 23 regions covering 17.566×10^{11} m^2 (Fig. 1). The central anchovy stock is enclosed by 8 regions (4, 5, 7, 8, 9, 11, 13, and 14) with a total of 5.703×10^{11} m^2 (Duke[3]). In this paper, I study the mortality of egg and larva of central anchovy stock. Anchovy eggs and larvae are sampled by net tows and each tow is a sampling unit. Every year, m_1 egg tows, vertical tows of 0.333 mm mesh with 25 cm diameter mouth opening, and m_2 larval tows using an oblique plankton net of 0.505 mm mesh with 60 cm diameter mouth opening are made. Ages were assigned to life stages using stage specific growth curves (Methot and Hewitt 1980[4]; Lo 1983). The standardized number of larvae in each group was divided by the time that larvae remained at a particular length to yield the sample mean daily larval production per unit area (0.05 m^2). A weighted mean per unit area for the entire survey area (8 regions) was calculated: $\bar{y}_i = \sum_r w_r\, \bar{y}_{ir}$ where w_r was the weight for region r and $\sum_r w_r = 1$ (Table 1) (Lo 1985) and $\bar{y}_{ir}$ was the sample mean count for i^{th} age group in region r. I considered only larvae smaller than 10 mm (20 d old) because for anchovy larvae larger than 10 mm, the

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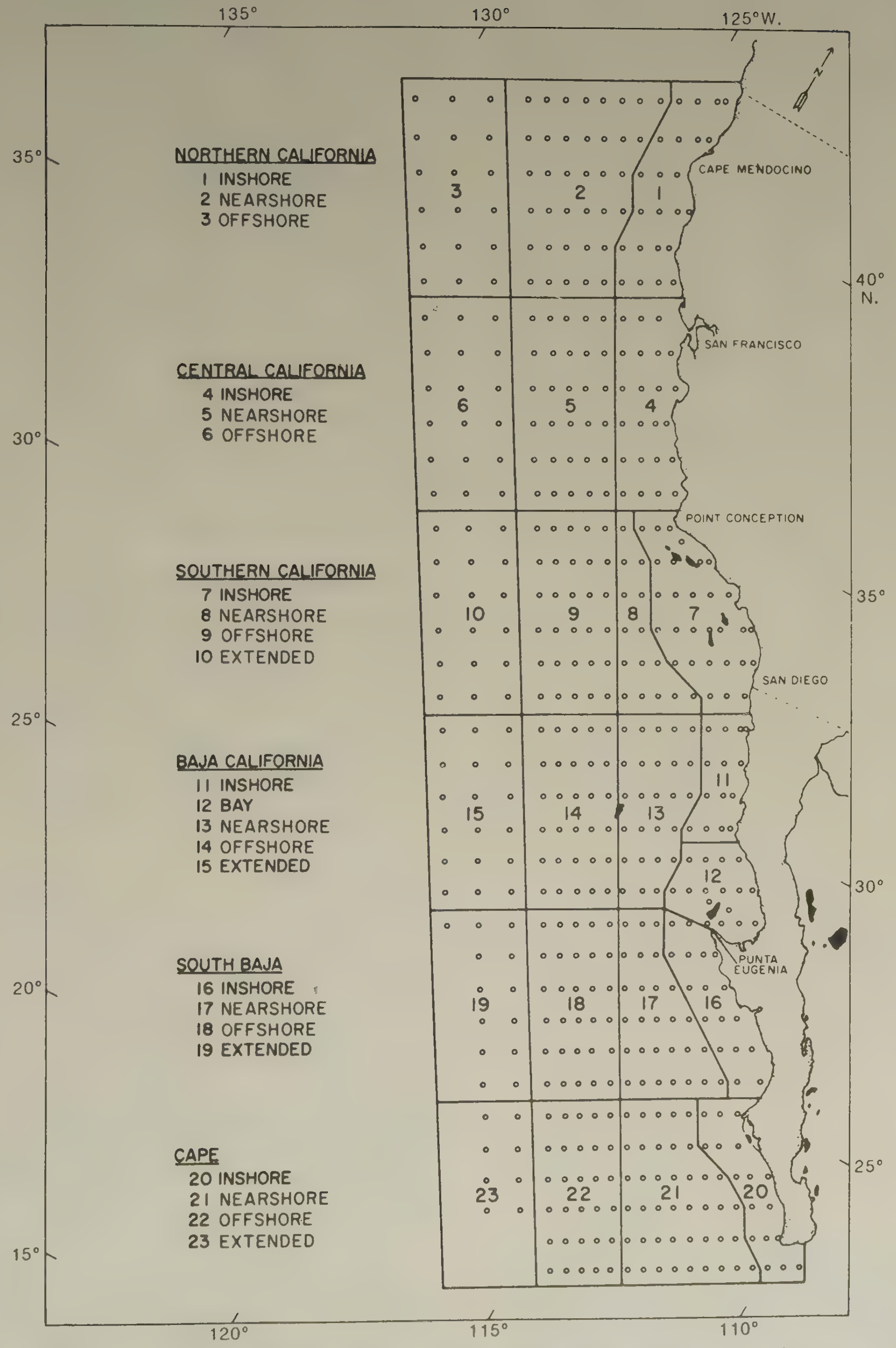
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3 OFFSHORE
CENTRAL CALIFORNIA
4 INSHORE
5 NEARSHORE
6 OFFSHORE
SOUTHERN CALIFORNIA
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8 NEARSHORE
9 OFFSHORE
10 EXTENDED
BAJA CALIFORNIA
11 INSHORE
12 BAY
13 NEARSHORE
14 OFFSHORE
15 EXTENDED
SOUTH BAJA
16 INSHORE
17 NEARSHORE
18 OFFSHORE
19 EXTENDED
CAPE
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21 NEARSHORE
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23 EXTENDED
CAPE MENDOCINO
SAN FRANCISCO
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FIGURE 1.—Sampling area for estimating mortality of northern anchovy eggs and larvae (<20 d) with sampling stations denoted by the open circles, and regions denoted by numbers.

TABLE 1.—Group data of anchovy eggs and larvae: Sample mean daily production ($\bar{y}_i$) at age t_i, days for regression estimators and sample mean daily death (n_i) for maximum likelihood estimators (MLEs) of egg and larval mortality.

1980						
Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	[1]n_i
1	0.41666	1.57	1	0.41666	1.57	
2	0.91666	1.21	2	0.91666	1.21	0.36
3	1.41666	1.07	3	1.41666	1.07	0.14
4	1.91666	0.64				
5	2.41666	0.88	4	2.1666	0.76	0.31
6	3.05	0.74	5	3.05	0.74	0.02
7	5.6	0.37	6	5.6	0.31	0.37
8	9.06	0.21	7	9.06	0.21	0.16
9	11.40	0.16	8	11.40	0.16	0.05
10	13.98	0.10	9	13.98	0.10	0.06
11	16.00	0.086	10	16.00	0.086	0.014
12	18.63	0.012	11	18.63	0.072	0.014

1981						
Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	n_i
1	0.41666	1.33				
			1	0.6666	1.665	
2	0.91666	2.00				
			2	1.6666	1.33	0.335
3	1.41666	1.19				
4	1.91666	1.47				
5	2.41666	1.11	3	2.41666	1.11	0.22
6	[2]2.91666	0.60				
			4	3.008	0.915	0.195
7	3.10	1.23				
8	5.98	0.44	5	5.98	0.44	0.475
9	9.45	0.25	6	9.45	0.25	0.19
10	11.97	0.16	7	11.97	0.16	0.09
11	14.37	0.10	8	14.37	0.10	0.06
12	16.53	0.10	9	16.53	0.10	0
13	18.56	0.08	10	18.56	0.08	0.02

1982						
Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	n_i
1	0.41666	0.84				
			1	0.6666	1.21	
2	0.91666	1.57				
3	1.41666	0.76				
			2	1.6666	0.93	0.28
4	1.91666	1.10				
5	2.41666	0.61				
			3	3.42	0.64	0.29
6	4.42	0.67				
7	8.00	0.23	4	8.00	0.23	0.41
8	11.07	0.14	5	11.07	0.14	0.09
9	13.62	0.08	6	13.62	0.08	0.06
10	15.74	0.06	7	15.74	0.06	0.02
11	18.13	0.05	8	18.13	0.05	0.01

1983						
Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	n_i
1	0.41666	1.78	1	0.41666	1.78	
2	0.91666	1.02				
			2	1.1666	1.67	0.11
3	1.41666	2.31				
4	1.91666	0.99	3	1.91666	0.99	0.68
5	2.41666	0.92	4	2.41666	0.92	0.07
6	3.82	0.68	5	3.82	0.68	0.24
7	7.03	0.16	6	7.03	0.16	0.52
8	9.97	0.11	7	9.97	0.11	0.05
9	12.34	0.08	8	12.34	0.08	0.03
10	14.60	0.05	9	14.60	0.05	0.03
11	16.73	0.0405	10	16.73	0.0405	0.01
12	18.88	0.0375	11	18.88	0.0375	0.003

[1] $n_i = \bar{y}_{i-1} - \bar{y}_i$. [2] Used in MLE only.

avoidance of the net becomes a serious bias.

Region	$nm^2 \times 10^{-3}$	$n^2 \times 10^{-10}$	w_r
4	18	6.105	0.107
5	29	9.878	0.174
7	20	6.896	0.119
8	12	4.116	0.072
9	29	9.878	0.174
11	9	3.171	0.054
13	21	7.122	0.125
14	29	9.866	0.174
Total	167	57.031	1.00

The sample mean daily production of eggs and larvae per 0.05 m² ($\bar{y}_i$) with its age (t_i) constituted the data base for regression estimates of IMRs of eggs and larvae in MEM and SEM. Mean daily production represent eggs for 0.17 d (4 h) $< t_i \leqslant 3$ d, and larvae for 3 d $< t_i \leqslant 20$ d; $i = 1, \ldots K$, where K is the total number of age groups. The sample age structure ($\bar{y}_i$, t_i) reflects that of a single cohort under the assumption of steady production over the survey period (Seber 1980). The same data set was also used to generate the sample mean number of eggs or larvae lost per day between two adjacent age groups ($n_i = \bar{y}_{i-1} - \bar{y}_i$). The statistics n_i's were used directly in the MLE. Normally, sample totals were used instead of sample means in MLE. I used n_i's because anchovy eggs and larvae were sampled with different nets and because the number of egg tows was different from that of larvae.

MULTI-EQUATION MODEL (MEM)

In the current estimation procedures, separate mortality curves are constructed (Equation (3)) for the IMRs ($\lambda(t)$) of anchovy eggs and larvae. If the life-stage-specific IMR is the main objective, the MEM is an easy method for obtaining the estimates of IMRs. The mortality curves (Equation (3)) are nonlinear functions of age (t). The IMRs can be estimated by either nonlinear regression (NR) or linear regression (LR) after the data set ($\bar{y}_i$, t_i) is transformed. The NR is based upon the assumption that the errors are additive. The observed mean daily production ($\bar{y}_i$) relates to the conditional survival probability as

$$\bar{y}_i = \theta_0 \, S_1[t_i;\, \lambda_1(t)] + e_{1i}$$

$$= \bar{y}_0 \, e^{-\alpha t_i} + e_{1i} \qquad t_i \leq u_1 \tag{4a}$$

$$\bar{y}_i = \theta_{u_1} \, S_1[t_i;\, \lambda_2(t)] + e_{2i}$$

$$= \bar{y}_{u_1}\left(\frac{t}{u_1}\right)^{-\beta} + e_{2i} \qquad u_1 \leq t_i \leq 20 \tag{4b}$$

where $u_1 = t_h \sim 3$ d old. Nonlinear regression estimation procedures provided by standard statistical packages such as BMDP statistical software (Dixon et al. 1983) are then used to estimate the parameters of IMRs, i.e., α and β.

The LR assumes that the errors are multiplicative. The observed daily production ($\bar{y}_i$) relates to the conditional survival probability in the form of

$$\bar{y}_i = \theta_{u_{g-1}} \, S_g(t_i;\, \lambda_g(t)) \, e_{gi} \qquad \text{for } g = 1,2.$$

The logarithm of both sides of the equation yields two linear functions

$$\ln(\bar{y}_i) = A - \alpha t_i + \epsilon_{1i} \qquad t_i \leq u_1 \tag{5a}$$

$$\ln(\bar{y}_i) = B - \beta \ln\left(\frac{t_i}{u_1}\right) + \epsilon_{2i} \qquad u_1 \leq t_i \leq 20. \tag{5b}$$

Equation (5a) is then fitted to data set ($\ln(\bar{y}_i)$, t_i for $t_i \leq u_1$), and Equation (5b) is fitted to data set ($\ln(\bar{y}_i)$, $\ln(t_i/u_1)$ for $u_1 \leq t_i \leq 20$ d) to estimate α and β.

SINGLE-EQUATION MODEL (SEM)

The SEM consolidates all the conditional survival probabilities ($S_g(t)$) from each mortality stanza into a single equation. It not only eliminates discontinuities at transitions between life stages, but also improves the precision of overall mortality estimates because of the large sample size. Moreover, the SEM makes it possible to estimate the IMR for life stages where data are scarce.

Based upon Equation (2), $S(t_i)$ of anchovy eggs and larvae is

$$S(t_i) = \begin{cases} S_1(t_i) & t_i \leq u_1 \\ S_1(u_1)S_2(t_i) & u_1 \leq t_i \leq 20 \end{cases}$$

or

$$S(t_i) = \begin{cases} S_1(t_i)S_2(u_1) & t_i \leq u_1 \\ S_1(u_1)S_2(t_i) & u_1 \leq t_i \leq 20 \end{cases}$$

where $S_1(u_1) = P(T > u_1|T \geq 0) = e^{-\alpha u_1}$, $S_2(u_1) = P(T > u_1|T \geq u_1) = 1$, and $u_1 = t_{ys} = 4.5$ d. Thus by creating two new independent variables x_{1i} and x_{2i} such that

$$x_{1i} = \begin{cases} t_i & t_i \leq u_1 \\ u_1 & u_1 \leq t_i \leq 20 \end{cases}$$

and

$$x_{2i} = \begin{cases} u_1 & t_i \leq u_1 \\ t_i & u_1 \leq t_i \leq 20 \end{cases}$$

it follows that $S(t_i) = S_1(x_{1i})S_2(x_{2i})$ and the mortality curve can be written as

$$E(\bar{y}_i) = \theta_0 S_1(x_{1i})S_2(x_{2i}) = \theta_0 e^{-\alpha x_{1i}}\left(\frac{x_{2i}}{u_1}\right)^{-\beta}. \tag{6}$$

The data set for fitting Equation (6) looks like

age group (i)	*age* (t_i)	$\bar{y}_i$	x_{1i}	x_{2i}	
1	t_1	$\bar{y}_1$	t_1	u_1	
2	t_2	$\bar{y}_2$	t_2	u_1	
.	.	.	.	.	
.	.	.	.	.	
.	.	.	.	.	
					$u_1 = 4.5$ d
i	t_i	$\bar{y}_i$	$\bar{u}_1$	t_i	
.	.	.	.	.	
.	.	.	.	.	
k	t_k	$\bar{y}_k$	$\bar{u}_1$	t_k	

In order to use Equation (6) to estimate the IMRs of eggs and larvae in Equation (1), a combined data set ($\bar{y}_1$, x_{1i}, x_{2i}), which includes all the data from each life stage and the maximum ages of mortality stanzas (u_g's), is important to ensure the accuracy of the estimates of the IMRs. The determination of u_g's depends primarily on the changes of the mortality rates, which may be related to the changes in morphology or behavior that affects mortality rates. In the best fit of the SEM, however, the end points of morphological patterns may not correspond to the maximum ages. Three life stages were identified for anchovy eggs and larvae, with the end point of mortality stanza 1 being the average age of yolk-sac larvae (u_1 = 4.5 d). In the MEM, the hatching time (t_h) was used, but, the best fit of the SEM occurred when u_1 = 4.5 d. Two mortality stanzas were assigned to three life stages of anchovy (<20 d) because from the existing data, no evidence for a change in the IMRs within a life stage existed although the data may not have been adequate to detect such changes.

The regression estimates of the IMRs for the SEM can be obtained by either NR or LR as described in the previous section. If NR is used, Equation (6) is fitted to the data set ($\bar{y}_i$, x_{1i}, and x_{2i}) directly to obtain estimates of parameters of $\lambda_1(t)$ and $\lambda_2(t)$. Because the variance of egg data is larger than that of larvae, a weighted NR (WNR) would be preferable. If errors are assumed to be multiplicative, taking the logarithm of both sides of the Equation (6) yields

$$\ln(\bar{y}_i) = A - \alpha x_{1i} - \beta \ln\left(\frac{x_{2i}}{u_1}\right) + \epsilon_i. \qquad (7)$$

The data set ($\ln(\bar{y}_i)$, x_{1i}, and $\ln(x_{2i}/u_1)$) is then used to estimate α and β through linear least squares regression.

MAXIMUM LIKELIHOOD ESTIMATOR (MLE)

The MLE is presented here as an alternative method of estimating IMRs. Because the data used for mortality estimators are grouped by age, I followed the procedures described by Kulldorff (1961) and McDonald and Ransom (1979) for grouped data. Here, $N_i = Y_{i-1} - Y_i$ (number of deaths between ages t_{i-1} and t_i) of a single cohort are multinomial variables, each with probability

$$P_i = S(t_{i-1}) - S(t_i).$$

The likelihood function of N_i's for the whole life cycle (i = 1, . . ., I, and Y_I = 0) is

$$L(N_i, P_i(z'); i = 1, \ldots, I) \propto \prod_{i=1}^{I} P_i(z')^{N_i}$$

$$= \prod_{i=1}^{I} [S(t_{i-1}) - S(t_i)]^{N_i} \qquad (8)$$

where z is the parameter vector in $\lambda(t)$. The derivatives of the logarithm of likelihood function with respect to the parameters z's are set equal to zero. Solutions to the simultaneous equations

$$\frac{\partial \ln L}{\partial z_i} = 0$$

are MLEs of z, if certain conditions are satisfied (Kulldorff 1961). In marine fish only the IMRs of a few life stages are considered because of the lack of data. It is then necessary to compute the conditional probability

$$P_i = P(t_{i-1} \leqslant T < t_i \mid T \in D)$$

$$= [S(t_{i-1}) - S(t_i)]/P(T \in D)$$

where D is the domain of ages of life stages considered.

Because I considered only the IMRs of anchovy eggs and larvae of ages >4 h (0.17 d) and <20 d, the conditional probabilities are computed from a truncated exponential and Pareto survival probability (Equation (2)) (Gross and Clark 1975, p. 128-132):

$$P_i = P(t_{i-1} < T \leqslant t_i \mid t_1 < T \leqslant 20)$$

$$= (S(t_{i-1}) - S(t_i))/(S(t_1) - S(20))$$

$$P_i = \begin{cases} \dfrac{e^{-\alpha t_{i-1}} - e^{-\alpha t_i}}{e^{-\alpha t_1} - e^{-\alpha u_1}\left(\dfrac{20}{u_1}\right)^{-\beta}} & t_i \leqslant u_1 \\[3ex] \dfrac{e^{-\alpha u_1}\left[\left(\dfrac{t_{i-1}}{u_1}\right)^{-\beta} - \left(\dfrac{t_i}{u_1}\right)^{-\beta}\right]}{e^{-\alpha t_1} - e^{-\alpha u_1}\left(\dfrac{20}{u_1}\right)^{-\beta}} & u_1 \leqslant t_i \leqslant 20. \end{cases} \qquad (9)$$

Then the likelihood function of N_i's for anchovy eggs and larvae of ages <20 d is

$$L \propto \prod_{i=2}^{k} P_i^{N_i} = \left[\prod_{i=2}^{k} (S(t_{i-1}) - S(t_i))^{N_i} \right] / \left[S(t_1) - S(20) \right]^{\sum_{i=2}^{k} N_i}$$

and

$$\ln(L) = \sum_{i=2}^{k} [N_i \ln(P_i)] = \sum_{i=2}^{c} [N_i \ln(P_i)] + \sum_{i=c+1}^{k} [N_i \ln(P_i)] \tag{10}$$

where $N_i = m(\bar{y}_{i-1} - \bar{y}_i) = m \cdot n_i$ and c is max(i) for $t_i \leqslant 3$ d (u_1). Substituting Equation (9) for P_i in Equation (10) yields

$$\ln(L) = \sum_{i=2}^{c} N_i \ln\left(e^{-\alpha t_{i-1}} - e^{-\alpha t_i}\right) + \sum_{c+1}^{k} \left[N_i(-\alpha u_1 + \beta \ln u_1) + N_i \ln(t_{i-1}^{-\beta} - t_i^{-\beta}) \right]$$

$$- \sum_{i=2}^{k} N_i \ln\left[e^{-\alpha t_1} - e^{-\alpha u_1} \left(\frac{20}{u_1}\right)^{-\beta} \right]. \tag{11}$$

Solving simultaneous equations $\dfrac{\partial \ln L}{\partial \alpha} = 0$ and $\dfrac{\partial \ln L}{\partial <}$ for α and β gives their MLEs.

The asymptotic variance-covariance (ASVAR-COV) of MLEs of α and β was computed according to Kulldorff (1961, p. 86-87):

$$\left.\begin{bmatrix} \text{As var}(\alpha) & \\ \text{As cov}(\alpha,\beta) & \text{As var}(\beta) \end{bmatrix}\right|_{\hat{\alpha},\hat{\beta}} = (1/N) \left.\begin{bmatrix} a_{11} & \\ a_{21} & a_{22} \end{bmatrix}\right|_{\hat{\alpha},\hat{\beta}} = (1/N)\, A_{\hat{\alpha},\hat{\beta}}$$

$$= -\frac{1}{N} \left.\begin{bmatrix} \sum_{i=2}^{k} P_i \dfrac{\partial^2 \ln P_i}{\partial \alpha^2} & \\ \sum_{i=2}^{k} P_i \dfrac{\partial^2 \ln P_i}{\partial \alpha \partial \beta} & \sum_{i=2}^{k} P_i \dfrac{\partial^2 \ln P_i}{\partial \beta^2} \end{bmatrix}^{-1}\right|_{\hat{\alpha},\hat{\beta}} \tag{12}$$

For detailed derivation of the MLEs, see the Appendix.

Conceptually, abundance declines monotonically with increasing age, but this may not occur in the sample. Although its absence does not complicate regression analysis, corrections are required when the MLEs are used. The MLEs are functions of sample totals $N_i = (\bar{y}_{i-1} - \bar{y}_i)m$, $N_i \geqslant 0$, and can also be expressed as function of sample proportions N_i/N (Equations (A1) and (A2)), which are equal to the ratios of differences of sample mean daily productions $(\bar{y}_{i-1} - \bar{y}_i)/(\bar{y}_1 - \bar{y}_k) = n_i/n$ (see Appendix). The quantity $n_i = N_i/m$ is the sample mean daily death between two adjacent groups. The MLEs require $N_i \geqslant 0$. Due to sampling error, it is possible to observe more individuals in the older group than the adjacent younger group, i.e., $\bar{y}_{i-1} < \bar{y}_i$. If so, some adjacent groups

$(\bar{y}_i, t_i)$ have to be combined so that $\bar{y}_i > \bar{y}_{i'}$ for $t_i < t_{i'}$. The ratio n_i/n can be used in place of N_i/N to compute the MLEs. This correction is inappropriate if the reason for $\bar{y}_i > \bar{y}_{i'}$, for $t_i < t_{i'}$ is that individuals were evicted from the sampling area or immigrated into it, as such movements violate the assumption of a stationary population.

Although n_i's are sufficient for computing point estimates of the MLE, the total number of deaths between ages t_1 and t_k ($N = m(\bar{y}_1 - \bar{y}_k)$) is required for computation of the ASVAR-COV of the MLEs. N can then be used to determine minimum number of tows (m_1) for the youngest stage through $m_1\bar{y}_1 \doteq N$ for a given precision of the MLE. Although the sample size for eggs may differ from that of larvae, an equal number of sample sizes is assumed to compute the ASVAR-COV. The minimum number of egg tows can be determined by $m_1 = N/\bar{y}_1$.

RESULTS

Both the MEM and the SEM were fitted to the basic data ($\bar{y}_i$, t_i; 0.17 d $< t_i \leqslant$ 20 d) collected from 1980 to 1983, using NR and LR (Table 1, Fig. 2). The point estimates and their asymptotic standard errors are listed in Table 2 and Figure 3. NR and LR produced similar estimates of the IMRs for the MEM. When the SEM was applied to the combined egg and larval data, the WNR was also used to compute the IMRs in addition to NR and LR because of the inequality of the variances among life stages. The variance of egg counts was higher than that of larvae because eggs were more patchily distributed than larvae. Because of this, the inverse of the variances of sample means of eggs and larvae was used as the weights for the WNR. The estimates from the WNR were similar to those from LR and the standard errors from both methods were lower than those from NR.

The WNR estimates of egg IMRs from the SEM were more precise than estimates from the MEM, whereas the most precise estimates of larval IMRs were provided by the MEM using NR. The SEM was more precise than the MEM for eggs but not for the larvae, because the variance of eggs was larger than that of larvae. Thus, when eggs and larvae were combined in an SEM, the variance around the single equation was smaller for the eggs and larger for the larvae. Nevertheless, the SEM produced larval IMRs with reasonable precision when the WNR was used. Therefore, the SEM WNR is suitable for ap-

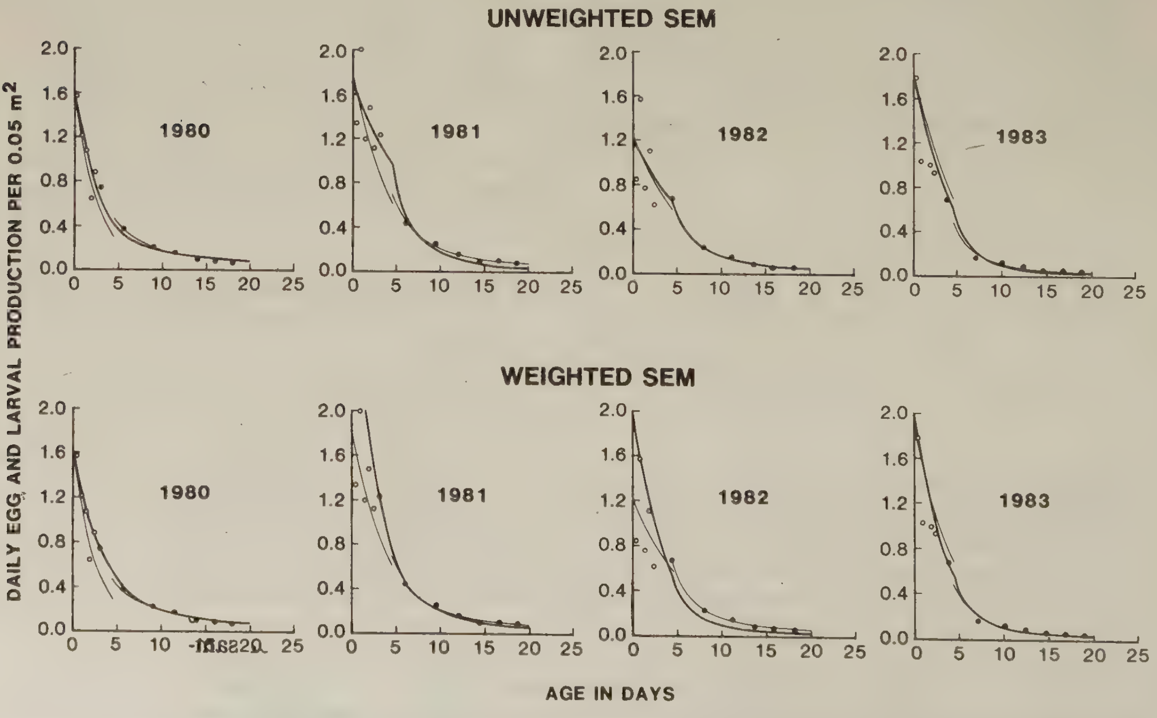

FIGURE 2.—Observed daily anchovy egg and larval production/0.05 m² (O = eggs, ● = larvae), and the mortality curves from the MEM (two short curves) and the SEM (one single curve) using unweighted and weighted nonlinear regression for 1980-83 field collected data.

TABLE 2.—Estimates from multi-equation model (MEM), single-equation model (SEM), and maximum likelihood estimator (MLE) for anchovy egg and larval mortality ($\hat{\alpha}$ and $\hat{\beta}$), and their standard error (SE) based upon 1980-83 field data where K is number of age groups and m is number of tows used in each model. For both MEM and SEM, nonlinear regression (NR), linear regression (LR) and weighted nonlinear regression (WNR) estimates are given.

	Egg mortality			Larval mortality		
	$\hat{\alpha}$	SE	$K(m)$	$\hat{\beta}$	SE	$K(m)$
1980						
MEM						
NR	0.39	0.103	5(961)	1.22	0.0314	7(199)
LR	0.35	0.13		1.32	0.06	
SEM						
NR	0.32	0.05	12(1,160)	1.06	0.41	12(1,160)
WNR	0.25	0.02		1.33	0.06	
LR	0.24	0.05		1.36	0.13	
MLE	0.36	0.012	11(961)	1.28	0.09	11(961)
		0.016	(500)		0.12	(500)
		0.02	(300)		0.16	(300)
		0.03	(199)		0.27	(199)
1981						
MEM						
NR	0.13	0.16	5(1,134)	1.53	0.032	7(403)
LR	0.13	0.15		1.54	0.06	
SEM						
NR	0.13	0.07	12(1,537)	2.19	0.96	12(1,537)
WNR	0.33	0.06		1.70	0.18	
LR	0.20	0.05		1.64	0.15	
MLE	0.24	0.008	10(1,134)	0.96	0.06	10(961)
		0.01	(500)		0.08	(500)
		0.02	(300)		0.11	(300)
		0.01	(403)		0.10	(403)
1982						
MEM						
NR	0.17	0.26	5(992)	1.81	0.036	6(96)
LR	0.19	0.24		1.87	0.065	
SEM						
NR	0.14	0.10	11(1,088)	1.77	1.46	11(1,088)
WNR	0.13	0.04		1.83	0.36	
LR	0.12	0.07		1.85	0.20	
MLE	0.24	0.008	8(992)	1.20	0.08	8(992)
		0.01	(500)		0.11	(500)
		0.015	(300)		0.14	(300)
		0.03	(100)		0.25	(100)
1983						
MEM						
NR	0.23	0.29	5(850)	2.05	0.11	7(78)
LR	0.27	0.25		1.80	0.10	
SEM						
NR	0.26	0.19	12(928)	2.45	2.71	12(928)
WNR	0.30	0.05		2.23	0.28	
LR	0.33	0.08		1.84	0.22	
MLE	0.32	0.007	11(850)	2.48	0.10	11(850)
		0.01	(500)		0.14	(500)
		0.013	(300)		0.18	(300)
		0.02	(80)		0.35	(80)

plications where it is preferable to estimate IMRs for egg and larvae simultaneously (e.g., simulation studies of mortality at all life stages). The SEM is preferable for modeling the mortality curves through all life stages because it eliminates the multiple estimates that occur at the endpoint of each life stage (Fig. 2). In addition, the SEM allows estimation of the IMRs for all life stages even when data for some life stages are inadequate for independent estimation of a life-stage-specific IMR. In comparing NR and LR, the estimates of IMRs from these two procedures were similar, despite the different assumptions about the error term. One complication of using LR is that the abundance for any

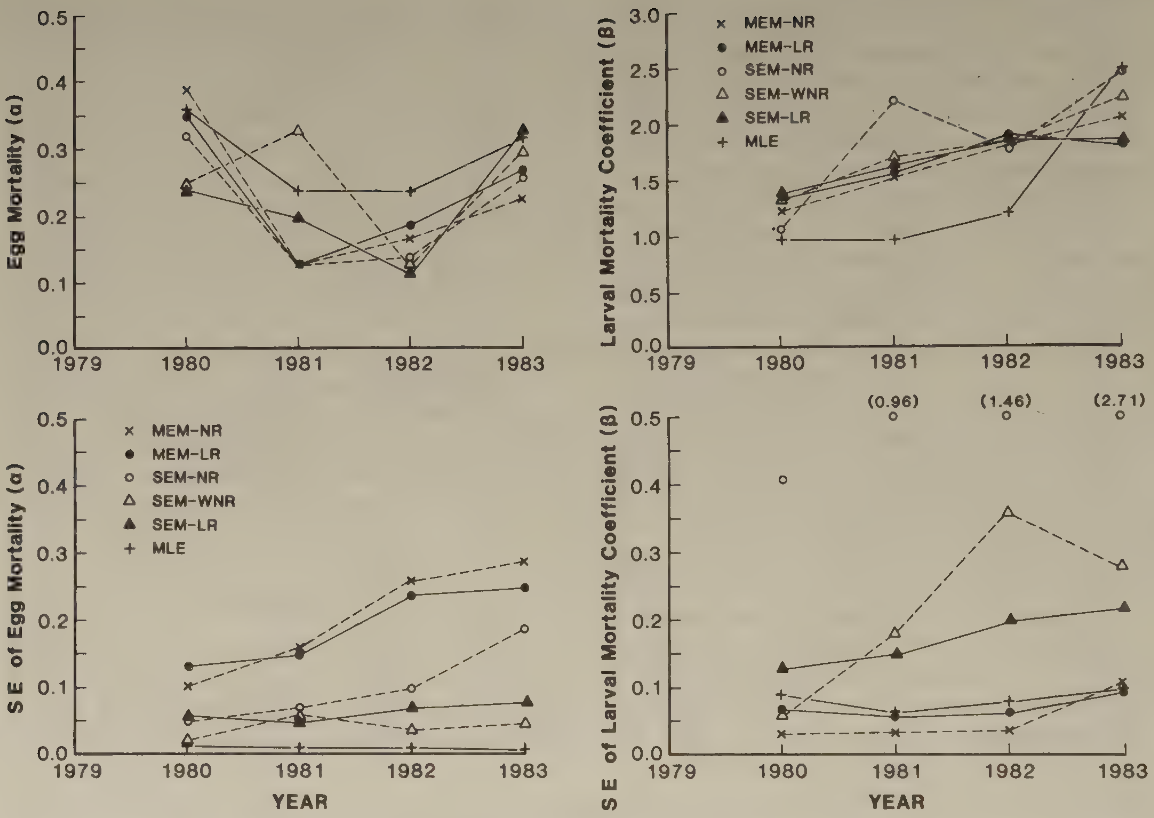

FIGURE 3.—Estimated anchovy egg mortality ($\hat{\alpha}$), larval mortality coefficient ($\hat{\beta}$), and their standard error (SE) using multi-equation model (MEM), single-equation model (SEM), and maximum likelihood estimator (MLE) for 1980-83.

specific age needs to be transformed back to the original unit. Direct inverse transformation may bias the estimates. Thus, the LR may not be appropriate for biomass estimation or other applications where a transformation back to original units is required.

In addition to the above regression models, the MLEs of egg and larval IMRs were also computed based on the data set $n_i = \bar{y}_{i-1} - \bar{y}_i$, $i = 1, \ldots k$ (Equations (A1) and (A2), Table 1). The ASCOV-VAR for anchovy egg and larval mortality rates requires the total number of eggs and larvae that died between ages 4 h and 20 d from the sample (N). It is not possible to obtain N directly from $m\bar{y}_1$ (i.e. $N \doteq m\bar{y}_1$) because eggs and larvae are sampled with different nets and in different regions. Anchovy eggs have a more concentrated and patchy distribution than larvae which are less numerous and distributed more uniformly throughout the entire survey area because of the diffusion of larvae after hatching (Hewitt 1982). Zero density of eggs was assumed for the offshore regions where eggs were not sampled to compute the weighted average egg production $\bar{y}_i = \sum_r w_r \bar{y}_{ir}$. I then divided $m_1\bar{y}_1$ by the proportion of area sampled ($q = \sum_r w_r$ where w_r's are summed over the regions where egg tows were taken) to obtain sample daily death N in $[t_1, t_k)$. Thus, $N = m_1\bar{y}_1/q$; q ranges from 0.53 to 0.82 for 1980-83. Four sets of sample sizes were considered: $m = m_1$, 500, 300, m_2 where m_1 is the actual number of egg tows and m_2, actual number of larval tows (Table 2). For any given N, one obtains the ASVAR-COV of α and β by dividing a_{ij} by N where a_{ij}'s are the elements in matrix A of Equation (12).

The MLE point estimates $\hat{\alpha}$ and $\hat{\beta}$, were between the estimates yielded by the SEM and the MEM in most cases. The precision of the MLE for egg IMR was higher than that of the regression estimates. The standard error of the MLE of the larval IMR was between those of the MEM and SEM regression estimates (Table 2, Fig. 3).

DISCUSSION

All the estimates of instantaneous mortality rates (IMR) discussed in this paper were computed from age (stage) frequency data. To ensure the unbiasedness of the estimates, three assumptions have to be met: a stationary population, reliable growth curves, and accurate samplers. Any violation of these assumptions will cause biases in the mortality estimates. Nets usually do not retain fish of all sizes because some small fish extrude through the net and some large fish avoid the net. Thus the estimates of size-specific retention rates are essential correction factors for the catch. If fish migrate at a significant rate, either the migration rate should be estimated or the sampling area should be expanded to eliminate migration problems, for migration violates the assumption of a stationary population and thus biases the mortality. Because growth curves are normally used to assign age to stage of eggs and larvae, biased growth curves would lead to inaccurate age assignments which definitely would bias the mortality estimates.

Although modeling the mortality rates of the early life stages of anchovy is the focus of this paper, I have shown that the SEM (Fig. 2) can be applied to any continuous process whose parameters are life-stage specific and generally estimated separately. For example, many allometric relations such as the growth curves may have different instantaneous growth rates for different life stages. A single continuous growth curve for the whole life cycle is possible using the SEM which allows greater latitude of modeling life-stage-specific growth rates than modeling the instantaneous growth rate for the whole life cycle as proposed by Schnute (1981). However, the SEM does require knowledge of the forms of instantaneous rates and the endpoint of each mortality stanza (or life stage).

In this study, the determination of a cutoff point between life stages was based upon examination of the empirical data and biological implications. It is conceivable to include the cutoff point (u_1) as one of the parameters in both SEM and MLE (Matthews and Farewell 1982). The cutoff point can then be estimated directly through the models. Matthews and Farewell considered the exponential mortality curve with one cutoff point and obtained MLE of the cutoff point (change point). For anchovy egg and larvae, the cuttoff point for the eggs and larvae up to 20 d old was easily determined from the IMR and age data (Lo 1985). Estimation of the cutoff point through SEM or MLE would be laborious and any improvement may be minimal. However, the estimates through the models would eliminate the problem of whether u_1 should be hatching time or the age of yolk-sac larvae.

Comparison of these two regression models with the MLEs based on anchovy egg and larval data indicated that the point estimates of the IMRs were similar. The SEM using WNR provided the most precise egg IMR which was nearly the same as the MLE. The MEM, using NR, provided the most precise estimates of larval IMR's. The regression estimators of the IMR's are easier to compute than the MLEs, yet they require larger sample sizes than the MLEs. If money is not a constraint, the SEM is preferred to the MLE. Otherwise, the MLE should be used. Based upon 1980 anchovy egg and larval data, 300 tows for eggs and larvae each (a total of 600 tows) could guarantee MLEs of α and β with cv = 0.10. The current sampling design (egg tows $\sim$ 1,000) seems to use an excessive number of egg tows for the MLEs of egg and larval IMRs. If the larval IMR is the only parameter to be estimated, the MEM is recommended.

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APPENDIX

The two partial deviations of ln L (Equation (11)) are

$$\frac{\partial \ln L}{\partial \alpha} = N \sum_{i=2}^{c} \frac{N_i}{N}\left[\frac{-t_{i-1} - t_i e^{-\alpha\Delta_i}}{1 - e^{-\alpha\Delta_i}}\right] - u_1 \sum_{i=c+1}^{k} \frac{N_i}{N} + t_1 - (u_1 - t_1)\left[e^{\alpha(u_1-t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^{-1} = 0 \quad \text{(A1)}$$

$$\frac{\partial \ln L}{\partial \beta} = N \sum_{i=c+1}^{k} \frac{N_i}{N}\left[\ln u_1 + \frac{-\ln t_{i-1} + \left(\frac{t_i}{t_{i-1}}\right)^{-\beta} \ln t_i}{1 - \left(\frac{t_i}{t_{i-1}}\right)^{-\beta}}\right] - \ln\left(\frac{20}{u_1}\right)\left[e^{\alpha(u_1-t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^{-1} = 0 \quad \text{(A2)}$$

where $\Delta_i = t_i - t_{i-1}$ and $u_1 \sim 3$.
Both Equations (A1) and (A2) depend on the proportion N_i/N rather than the absolute counts (N_i's). In order to have a unique solution of α and β, it is necessary to have

$$\frac{\partial^2 \ln L}{\partial \alpha^2} < 0 \quad \text{and} \quad \frac{\partial^2 \ln L}{\partial \beta^2} < 0. \qquad \text{(A3)}$$

Moreover, the conditions

$$\lim_{\alpha \to 0} \frac{\partial \ln L}{\partial \alpha} > 0, \quad \lim_{\alpha \to \infty} \frac{\partial \ln L}{\partial \alpha} < 0$$

and (A4)

$$\lim_{\beta \to 0} \frac{\partial \ln L}{\partial \beta} > 0, \quad \lim_{\beta \to \infty} \frac{\partial \ln L}{\partial \beta} < 0$$

guarantee a positive solution of α and β. Equation (A3) leads to the following constraints

$$1 < \frac{\left[e^{\alpha(u_1-t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}{(u_1 - t_1)^2\left(\frac{20}{u_1}\right)^{\beta} e^{(u_1-t_1)\alpha}} \sum_{i=2}^{c} \frac{N_i}{N}\left(\frac{t_i - t_{i-1}}{1 - e^{-\alpha(t_i-t_{i-1})}}\right)^2 e^{-\alpha(t_i-t_{i-1})} \tag{A5}$$

and

$$1 < \frac{\left[e^{\alpha(u_1-t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}{\left[\ln\left(\frac{20}{u_1}\right)\right]^2\left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1-t_1)}} \sum_{i=c+1}^{k} \frac{N_i}{N} \frac{\left(\frac{t_i}{t_{i-1}}\right)^{-\beta}\left[\ln \frac{t_i}{t_{i-1}}\right]^2}{\left[1 - \left(\frac{t_i}{t_{i-1}}\right)^{-\beta}\right]^2}. \tag{A6}$$

After algebraic manipulation, it was easy to see that Equation (A4) was true for this truncated exponential and the Pareto MLE. We used an iterative procedure to select the MLE of α and β, which satisfies not only Equation (A3) but also the constraints of Equations (A5) and (A6).

The partial derivations in each entry of matrix A (Equation (12)) are

$$\frac{\partial^2 \ln P_i}{\partial \alpha^2} = -\left(\frac{\Delta_i}{e^{\alpha\Delta_i} - 1}\right)^2 e^{\alpha\Delta_i} + (u_1 - t_1)^2 \frac{\left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1-t_1)}}{\left[e^{\alpha(u_1-t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}$$

$$\frac{\partial^2 \ln P_i}{\partial \beta^2} = \frac{\left[\ln\left(\frac{20}{u_1}\right)\right]^2\left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1-t_1)}}{\left[e^{\alpha(u_1-t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}$$

and

$$\frac{\partial^2 \ln P_i}{\partial \alpha \partial \beta} = \frac{(u_1 - t_1)\left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1-t_1)} \ln\left(\frac{20}{u_1}\right)}{\left[e^{\alpha(u_1-t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}.$$

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INCIDENTAL MORTALITY OF DOLPHINS IN THE EASTERN TROPICAL PACIFIC, 1959-72

N. C. H. Lo[1] and T. D. Smith[2]

ABSTRACT

The estimates of the number of dolphins killed annually from the beginning of the U.S. tuna purse seine fishery in the eastern tropical Pacific are used by the National Marine Fisheries Service in developing management advice for the U.S. purse seine fleet. We estimated the annual number of dolphins killed incidentally in the tuna purse seine fishery for 1959-72. Kill data were available for only a few years prior to 1970. Because no obvious trend was shown with the existing data, kill rates were averaged over those years and stratified by various categories: large and small vessels, sets with large catch of tuna and small catch of tuna, sets which used backdown (a dolphin-releasing procedure), and sets which did not use backdown. These kill rates, combined with estimated number of sets, produced the estimated annual kills. Because data were available only for some of the years, they had to be pooled to obtain annual estimates. As a result, the annual estimates were highly correlated. Because the total as well as the annual estimates are of interest, it is necessary to compute the variance-covariance of the estimated annual kills. The annual kill from 1959 to 1972 varied from 55,000 in 1959 to 534,000 in 1961. There were three distinct maxima of 534,000, 460,000, and 467,000, corresponding to peaks in number of sets made on dolphins in 1961, 1965, and 1970. The total kill from 1959 to 1972 was estimated to be about 4.8 million, with a coefficient of variation of 17%.

The eastern tropical Pacific tuna purse seine fleet began to develop rapidly in the late 1950's and has grown to over 100 U.S.-registered vessels and a substantial number of non-U.S.-registered vessels in recent years. This fleet fishes primarily for yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*. Majority of the yellowfin tuna are taken while the tunas are schooling with dolphins primarily of the species *Stenella attenuata* and *S. longirostris*. Birds and dolphins are frequently used as cues in finding the tuna. During the capture of the tuna, some of the dolphins are killed or drowned by becoming tangled in the net webbing (Perrin 1969). The number of dolphins killed has been estimated to have been greater than one-half million in some of the years in the 1960's (Smith 1983). Currently, fewer animals are killed each year due to improvements in the fishing gear and in procedures to release dolphins.

Estimates of the total number of dolphins killed each year in this fishery are used as a basis for management advice by the National Marine Fisheries Service (NMFS). In this paper we describe in detail the method used in Smith (1983), including estimation of the variances and covariances of the annual kill estimates so that the variance of the total kill for the period can be estimated. Additionally, we reexamine the data used in previous estimates (Perrin 1970; Perrin and Zweifel 1971[3]; Perrin et al. 1982; Smith 1983; Smith and Lo 1983), and we present revised estimates of the total numbers of dolphins killed.

MATERIALS AND METHODS

The model used to estimate the total annual incidental kill of dolphins (T_t) in the eastern tropical Pacific tuna purse seine fishery is

$$\hat{T}_t = \hat{R}_t \hat{X}_t \qquad (1)$$

where t denotes the year (1959 to 1972), R denotes the number of dolphins killed per set, and X denotes the number of sets made involving dolphins. The rate of kill (R) varies between larger and smaller vessels, and in dolphin sets where fewer and greater amounts of yellowfin tuna are caught (Lo et al. 1982). In addition, the rate of dolphin kills is generally less if

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[3] Perrin, W. F., and J. R. Zweifel. 1971. Porpoise mortality in the eastern tropical tuna fishery in 1971. Unpubl. manuscr., 22 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

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backdown, a dolphin-release procedure, is used (Green et al. 1971; Barham et al. 1977; Smith and Lo 1983). To account for these factors affecting rates of dolphin kill, Equation (1) can be reexpressed with the rates and numbers of sets stratified by vessel tuna carrying capacity, catch of fish, and use of backdown procedure:

$$\hat{T}_t = \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \hat{R}_{tijk} \hat{X}_{tijk} \tag{2}$$

where t = year
i = 1 for vessel capacity >600 tons; 2 for vessel capacity ≤600 tons
j = 1 for yellowfin tuna catch ≥¼ ton; 2 for yellowfin tuna catch <¼ ton
k = 1 backdown is used; 2 backdown is not used.

Data on the number of dolphins killed during fishing trips in the period from 1964 to 1968 are given in Smith and Lo (1983). Similar but more extensive data (e.g., backdown information) are available in NMFS records for 1971 and 1972. Estimates on the number of sets involving dolphins from 1959 to 1972 are given by Punsley (1983). These data sources have certain limitations which do not allow for the use of the complete stratification scheme in Equation (2). Assumptions are made based on sample sizes and on apparent lack of changes in rates over time to accommodate these limitations.

The mean numbers of dolphins killed (kill-per-set) are shown in Table 1 for each year in which data are available, stratified by vessel size and by catch of fish (successful, ≥¼ ton of yellowfin tuna; unsuccessful, <¼ ton of yellowfin tuna). The definition of successful set follows that of Perrin and Zweifel (fn. 3). The vessel class stratification was based on the vessel's fish carrying capacity. The 1964-74 kill data indicate that kill-per-set was different for vessels with ≤600 tons carrying capacity and vessels with >600 tons for unsuccessful sets. For successful sets the optimal vessel class stratification was not clear; either 400, 600, or 800 tons can be used as division points for stratification. For consistency, we adopted the same stratification used for unsuccessful sets. (The results were similar with alternative stratification schemes.) Other factors such as the age of the vessel and the experience of the captain could affect kill rates but were not considered in the stratification because these factors could not be isolated for analysis.

The mean number of dolphins killed varied markedly over the years but without any obvious trends (Table 1). A two-way analysis of variance with the data pooled over years showed statistically significant differences in kill rates in sets made by small and large vessels ($P < 0.01$) and in successful and unsuccessful sets ($P < 0.01$). Thus Equation (2) was simplified by eliminating the time stratification for kill rates, whereas the vessel size and catch strata were retained.

Few observations are available for sets where backdown was not used. In successful sets, backdown was used more than 90% of the time; thus, we have observations on kill rates in only 20 sets where backdown was not used. Thirteen of these sets were made by large vessels and seven by small vessels, and the mean kill rates within vessel size class are highly variable and not significantly different. The overall ratio of the kill rates, pooled over vessel size, when backdown was not used and when it was used is significantly greater than unity, and the annual

TABLE 1.—Average numbers of dolphins killed (*M*) in purse seine sets in the eastern tropical Pacific by year, for small and large vessels making successful (>¼ ton tuna) and unsuccessful (≤¼ ton tuna) net sets. Standard deviation (SD), number of sets (*N*), and number of trips are given.

Vessels and year	Successful sets				Unsuccessful sets				Data source
	M	SD	*N*	No. of trips	*M*	SD	*N*	No. of trips	
Small vessels (≤600 tons carrying capacity)									
1964	60	47	20	1	60	—	1	1	Smith and Lo (1983)[1]
1965	26	28	35	1	3	8	11	1	Smith and Lo (1983)
1968	130	114	13	1	4	4	2	1	Smith and Lo (1983)
1971	117	180	19	3	13	10	3	2	Unpubl. NMFS
1972	57	110	103	6	4	10	16	5	Unpubl. NMFS
Total	62	108	190	12	6	13	33	10	
Large vessels (>600 tons carrying capacity)									
1971	41	56	16	2	—	—	—	0	Unpubl. NMFS
1972	37	123	117	6	0.4	1.4	12	5	Unpubl. NMFS
Total	37	119	133	8	0.4	1.4	12	5	

[1] From table 5 of Smith and Lo (1983), omitting incomplete data collected in 1966.

ratios vary without a consistent trend over time (Table 2).

In unsuccessful sets the use of the backdown procedure was more variable because the conditions of the set are more diverse. For example, only a few or no dolphins may be captured, and the net may not be retrieved in the usual manner. Because of this diversity and because so few observations are available, we consider one kill rate for all unsuccessful sets.

Reexpressing Equation (2) to account for a constant ratio of kill rates for successful sets when backdown was used and when it was not used, and for no difference in kill rates for unsuccessful sets, yields

$$\hat{T}_t = \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \hat{R}_{\bullet ijk} \hat{X}_{tijk}$$

$$= \sum_{i=1}^{2} \{\hat{R}_{\bullet i11} (\hat{X}_{ti11} + C\hat{X}_{ti12}) + \hat{R}_{\bullet i2\bullet} \hat{X}_{ti2\bullet}\} \qquad (3)$$

where $C = R_{\bullet\bullet 12}/R_{\bullet\bullet 11}$ and the subscript $\bullet$ is used when that stratifying variable is not considered. For example, $R_{\bullet ijk}$ is the kill-per-set not stratified by year t, and $X_{ti2\bullet}$ is the total number of sets not stratified by use of backdown.

Estimates of the total number of sets involving dolphins from 1959 to 1972, with approximate variances, are given by Punsly (1983). He also gives partial estimates of the numbers of successful and unsuccessful sets, but does not provide estimates of the numbers of sets by vessel size. Punsly's data did not indicate the use of the backdown procedure.

The coefficients of variation (CV) of Punsly's estimates are ≤1% in all years except 1959 and 1960, when it was 8%. The percentage of unidentified sets in 1959-61 was higher than subsequent years because set type was not recorded systematically (Hammond[4]). We assume these estimates are in fact constants, because in most years, and in the absence of additional information in 1959-61, the CVs are small compared with the CVs of the kill rates (0.13-1.0, Table 1).

By applying the proportions of successful and unsuccessful dolphin sets from Punsly's partial estimates to his totals, we obtained numbers of successful and unsuccessful dolphin sets. We further prorate these estimated numbers of successful and unsuccessful sets to large and small vessels by multiplying by the estimates of proportions from NMFS (Anonymous 1976[5]) of sets made by vessels of each size class (Table 3). The slight differences between the totals for each year given by Punsly are due to rounding.

The number of sets during which backdown was used can be estimated from the estimated total number of sets involving dolphins (Table 3) and the observed proportion of successful sets in which backdown was used (Table 2). The observed proportions increase from 0.79 in 1964-65 to almost unity (0.96) by 1972. The backdown procedure was reportedly

TABLE 2.—Mean number of dolphins killed ($\hat{R}$) during purse seine sets in the eastern tropical Pacific Ocean when the backdown dolphin-release procedure was and was not used. Also given are the ratio of numbers killed with and without backdown ($\hat{C}$), the proportion of successful sets where backdown was used ($\hat{P}$), the number of sets (N), number of trips, and standard error in parentheses.

	Backdown used							
	Yes			No				
Year	$\hat{R}_{t\bullet 11}$	N	No. of trips	$\hat{R}_{t\bullet 12}$	N	No. of trips	$\hat{C}$	$\hat{P}$
1964[1]	44	16	1	128	4	1	3.0	0.79
1965[1]	48	6	1	24	2	1	0.50	
1966[1,2]	—	17	1	—	2	1	—	0.89
1968[1]	142	11	1	92	1	1	0.65	
1971[3]	81	30	5	111	4	3	1.40	
1972[3]	41	193	12	169	9	6	4.10	0.96
Total	50	256	21	131	20	12	2.62 [4](0.80)	0.93

[1] From Smith and Lo (1983).
[2] Kill rates for 1966 omitted because incomplete data were collected.
[3] NMFS records.
[4] $SE(\hat{C}) = \hat{C}\,[CV^2(\hat{R}_{\bullet\bullet 12}) + CV^2(\hat{R}_{\bullet\bullet 11}) - 2\,\mathrm{cor}(\hat{R}_{\bullet\bullet 12}, \hat{R}_{\bullet\bullet 11})]^{1/2}$; where $\hat{C} = \hat{R}_{\bullet\bullet 12}/\hat{R}_{\bullet\bullet 11}$.

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[4] P. S. Hammond, Sea Mammal Research Unit, British Antarctic Survey, Cambridge, England, pers. commun. 1983.

[5] Anonymous. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery (La Jolla, July 27-31, 1976). Southwest Fish. Cent., Admin. Rep. LJ-76-29, 54 p. + app.

TABLE 3.—Numbers of purse seine sets involving dolphins in the eastern Pacific Ocean, from 1959 to 1972, for small (≤600 tons) and large (>600 tons) vessels, and for successful (>¼ tons tuna) and unsuccessful (≤¼ tons) sets, modified from Punsly (1983).

	Successful sets		Unsuccessful sets	
Year	small ($X_{t21\bullet}$)	large ($X_{t11\bullet}$)	small ($X_{t22\bullet}$)	large ($X_{t12\bullet}$)
1959	326	0	265	0
1960	3,170	0	2,303	0
1961	3,888	32	3,928	0
1962	1,773	5	1,942	19
1963	2,291	10	2,092	23
1964	4,444	45	3,089	64
1965	5,346	27	2,418	29
1966	4,948	44	1,835	25
1967	3,363	2	841	3
1968	2,956	175	982	41
1969	5,365	1,401	1,402	192
1970	4,936	2,313	957	412
1971	1,871	2,602	652	409
1972	2,704	4,982	855	846

developed on one vessel in 1959-60 (Barham et al. 1977) and used by at least three vessels in 1961 (Anonymous 1962). If 79% of the sets in 1964-65 were made using this procedure, as suggested by the very limited available data, a rather rapid increase in usage must have occurred in 1962 and 1963. This is possible because, if properly used, the procedure reduces the amount of handling time of dead dolphins, thus speeding up the fishing operation. As an approximation, we assume that usage increased from 0 to 0.79 linearly from 1959 to 1964-65, and was 0.89 for 1966-71 and 0.96 for 1972.

Denoting the interpolated and extrapolated estimates of the proportion of successful sets using the backdown dolphin release procedure by P_t gives

$$\hat{X}_{ti11} = \hat{P}_t \hat{X}_{ti1\bullet}$$

$$\hat{X}_{ti12} = (1 - \hat{P}_t)\, \hat{X}_{ti1\bullet}.$$

Substituting these relationships into Equation (3), with the assumption that the estimated numbers of sets given by Punsley (1983) are constants, the following equations result when the terms are rearranged:

$$\hat{T}_t = \sum_i \left\{\hat{R}_{\bullet i11}[X_{ti1\bullet}\hat{P}_t + C(1 - \hat{P}_t)X_{ti1\bullet}] + R_{\bullet i2\bullet}X_{ti2\bullet}\right\}$$

$$= \sum_i \left\{\hat{R}_{\bullet i11}X_{ti1\bullet}[\hat{P}_t + C(1 - \hat{P}_t)] + \hat{R}_{\bullet i2\bullet}\, X_{ti2\bullet}\right\}. \qquad (4)$$

The time series of estimated annual kill ($\hat{T}_t$) from 1959 to 1972 was obtained by pooling the available data over years and strata, resulting in estimates that are not statistically independent. Thus in order to estimate the variance of the total kill of dolphins for the period in addition to the variances it is necessary to determine the covariances among the annual estimates.

We denote the estimates of the total kill of dolphins ($\hat{T}_t$) for each year from 1959 to 1972 by the vector $\hat{T}$, and denote the estimates of the variances of the elements of $\hat{T}$ by the symmetric matrix $\Sigma_{\hat{T}}$. The estimate of the kill in each year (Equation (4)) can be expressed in matrix form as the product of a vector of the numbers of sets in each of the four combinations of the vessel size and fishing success classifications (X_t), and a vector of the four corresponding kill rates (Q_t). Each element of $\hat{T}$ then can be expressed as a matrix product

$$\hat{T}_t = X'_t\, \hat{Q}_t \qquad (5)$$

where $X'_t = (X_{t11\bullet}, X_{t21\bullet}, X_{t12\bullet}, X_{t22\bullet})$

$$\hat{Q}_t = \begin{bmatrix} \hat{Q}_{t1} \\ \hat{Q}_{t2} \\ \hat{Q}_{t3} \\ \hat{Q}_{t4} \end{bmatrix} = \begin{bmatrix} \hat{R}_{\bullet 111}[\hat{P}_t(1 - \hat{C}) + \hat{C}] \\ \hat{R}_{\bullet 211}[\hat{P}_t(1 - \hat{C}) + \hat{C}] \\ \hat{R}_{\bullet 12\bullet} \\ \hat{R}_{\bullet 22\bullet} \end{bmatrix} = \begin{bmatrix} \hat{R}_{\bullet 111}\, f_t \\ \hat{R}_{\bullet 211}\, f_t \\ \hat{R}_{\bullet 12\bullet} \\ \hat{R}_{\bullet 22\bullet} \end{bmatrix} \text{ and } f_t = \hat{P}_t(1 - \hat{C}) + \hat{C}.$$

Then the variance-covariance matrix of $\hat{T}$ is

$$\Sigma_{\hat{T}} = \begin{bmatrix} V(\hat{T}_{59}) & & & \\ \mathrm{Cov}(\hat{T}_{59}, \hat{T}_{60}) & V(\hat{T}_{60}) & & \\ \vdots & \vdots & & \\ \mathrm{Cov}(\hat{T}_{59}, \hat{T}_{72}) & \mathrm{Cov}(\hat{T}_{60}, \hat{T}_{72}) & \ldots & V(\hat{T}_{72}) \end{bmatrix}$$

$$= \begin{bmatrix} V(X'_{59}\, Q_{59}) & & & \\ \mathrm{Cov}(X'_{59}\, Q_{59}, X'_{60}\, Q_{60}) & V(X'_{60}\, Q_{60}) & & \\ \vdots & \vdots & & \\ \mathrm{Cov}(X'_{59}\, Q_{59}, X'_{72}\, Q_{72}) & \mathrm{Cov}(X'_{60}\, Q_{60}, X'_{72}\, Q_{72}) & \ldots & V(X'_{72}\, Q_{72}) \end{bmatrix}$$

with $V(\hat{T}_t) = X'_t\, \Sigma_{\hat{Q}_t} X_t$
as the diagonal elements of $\Sigma_{\hat{T}}$ (6)

$$\text{where } \Sigma_{\hat{Q}_t} = \begin{bmatrix} V(\hat{R}_{\bullet 111} f_t) & \mathrm{Cov}(\hat{R}_{\bullet 111} f_t, \hat{R}_{\bullet 211} f_t) & 0 & 0 \\ & V(\hat{R}_{\bullet 211} f_t) & 0 & 0 \\ & & V(\hat{R}_{\bullet 21 \bullet}) & 0 \\ & & & V(\hat{R}_{\bullet 22 \bullet}) \end{bmatrix} . \qquad (7)$$

The diagonal elements of $\Sigma_{\hat{T}}$ can be computed by noting that $\hat{R}_{\bullet i2\bullet}$ is uncorrelated with $\hat{R}_{\bullet i11}$, $\hat{P}_t$, or $\hat{C}$, and the covariance of $\hat{P}_t$ and $\hat{C}$ is zero because one C value is used for all years in 1959-72 and $\hat{P}_t$ can be different between years.

The off-diagonal elements of $\Sigma_{\hat{T}}$ are

$$\mathrm{Cov}(\hat{T}_u, \hat{T}_m) = \mathrm{Cov}(X'_u \hat{Q}_u, X'_m \hat{Q}_m) \qquad (8)$$

$$= \sum_{i=1}^{4} \sum_{j=1}^{4} X_{ui}\, \mathrm{Cov}(\hat{Q}_{ui}, \hat{Q}_{mj})\, X_{mj}.$$

Expressions for each of the terms in $\Sigma_{\hat{T}}$ are given in the Appendix.

RESULTS AND DISCUSSION

The estimates of the total number of dolphins killed incidentally in the tuna purse seine fishery from 1959 to 1972 (Table 4, from Equation (4)) vary from a low of 55,000 in 1959 to a high of 534,000 in 1961. Three distinct maxima of 534,000, 460,000, and 467,000 are apparent (Fig. 1), corresponding to peaks in numbers of sets made on dolphins in 1961, 1965, and 1970 (Table 3). A total of about 4.8 million dolphins is estimated to have been killed in the whole period (Table 4).

The CVs of the annual estimates decline rapidly

TABLE 4.—Estimated number of dolphins killed by year (Equation (4)), with standard errors (SE) and coefficient of variations (CV).

Year	Number killed	SE	CV
1959	55,000	18	0.32
1960	478,000	146	0.31
1961	534,000	149	0.28
1962	216,000	54	0.25
1963	240,000	54	0.22
1964	390,000	77	0.20
1965	460,000	92	0.20
1966	374,000	58	0.15
1967	257,000	39	0.16
1968	229,000	35	0.15
1969	461,000	68	0.15
1970	467,000	70	0.15
1971	254,000	43	0.17
1972	380,000	61	0.16
1959-72	4,790,000	857	0.18

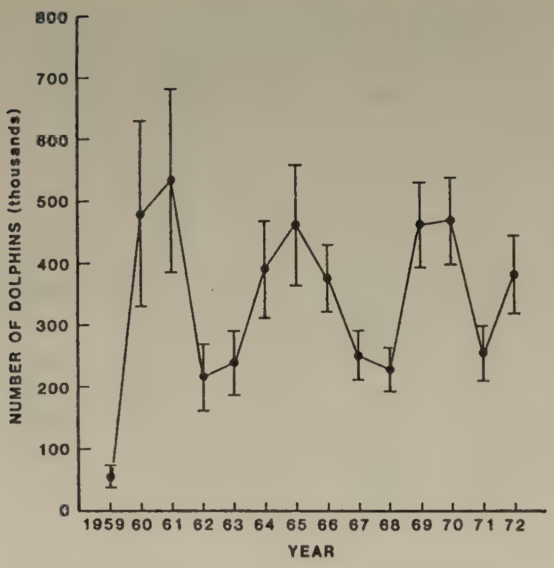

FIGURE 1.—Estimated numbers of dolphins killed in the eastern tropical Pacific tuna purse seine fishery from 1959 to 1972. Standard errors of the estimates shown as vertical bars. From Table 4.

from 32% in 1959 to 15% from 1966 to 1970, and then increase only slightly in 1971 and 1972. The covariances are large (upper triangular matrix, Table 5). They are all positives, and tend to be smaller for pairs of estimates widely spaced in time. The covariances can be examined more easily in terms of correlation coefficients (lower triangular matrix, Table 5). The correlations range from 0.31 to 0.99. The CV of the estimated total is 18%. This is substantially higher than the corresponding value of 6% obtained when the covariances are ignored. Because the total is the sum of 14 numbers, an approximate 95% confidence interval, obtained by adding and subtracting two standard errors, is 3.1-6.5 million dolphins.

The variation in the estimated numbers of dolphins killed over the period 1959-72 is due to several factors: 1) The number of sets made involving dolphins varied from year to year depending on the number of sets of tuna schooling in the absence of dolphins; such tuna are apparently preferred when available. 2) The use of the backdown dolphin-release procedure increased rapidly from 1959 to 1964. However, the development of the backdown dolphin-release procedure is not well known. The available data reflect the tendency of captains to use the technique once it was known. There is little information on how rapidly the procedure became known to other captains and no information on how rapidly they learned to use it effectively. Our assumption of a linear increase probably overestimates the use of backdown initially, but may or may not overestimate its subsequent use. 3) The proportion of successful sets made by small vessels increased from about 50% from 1959 to 1964, to >75% from 1965 to 1972 (Table 1). The higher dolphin kill rate for successful sets results in an increase in estimated dolphin kills as the proportion of successful sets increased. 4) The increase in the proportion of sets which were made by large vessels starting in 1968 results in a decrease in estimated dolphin kill rates due to the lower dolphin kill rate of these vessels.

Several factors which may have affected the numbers of dolphins killed in this period have not been accounted for because of the assumptions made by incomplete data. Chief among these assumptions were 1) the relatively small samples are representative of the fleet as a whole, 2) the kill rates on unsuccessful sets are not affected by the use of backdown, 3) the ratio of kill-per-set in successful sets without backdown to that with backdown is constant

TABLE 5.—Covariances (upper triangular matrix, x10^{10}) and correlation coefficients (lower triangular matrix) for the estimated total dolphins killed by year, from 1959 to 1972.

	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972
1959		0.41	0.42	0.14	0.13	0.16	0.15	0.11	0.07	0.06	0.13	0.13	0.06	0.04
1960	0.99		3.49	1.24	1.15	1.37	1.32	0.92	0.62	0.56	1.10	1.08	0.54	0.40
1961	0.99	0.99		1.27	1.19	1.45	1.38	0.95	0.64	0.57	1.13	1.11	0.55	0.42
1962	0.97	0.98	0.99		0.44	0.55	0.52	0.34	0.23	0.21	0.41	0.40	0.19	0.15
1963	0.92	0.94	0.96	0.98		0.58	0.53	0.33	0.22	0.20	0.39	0.38	0.18	0.15
1964	0.76	0.79	0.83	0.88	0.95		0.75	0.43	0.29	0.26	0.50	0.49	0.23	0.20
1965	0.79	0.81	0.84	0.88	0.92	0.93		0.56	0.34	0.27	0.51	0.50	0.23	0.20
1966	0.65	0.66	0.67	0.67	0.67	0.62	0.86		0.30	0.21	0.39	0.38	0.17	0.16
1967	0.75	0.76	0.77	0.78	0.78	0.71	0.89	0.93		0.16	0.30	0.29	0.13	0.10
1968	0.74	0.75	0.76	0.77	0.76	0.70	0.77	0.69	0.90		0.31	0.30	0.14	0.10
1969	0.73	0.74	0.75	0.76	0.75	0.68	0.75	0.66	0.87	0.98		0.63	0.33	0.27
1970	0.71	0.72	0.73	0.73	0.72	0.65	0.70	0.62	0.83	0.94	0.98		0.36	0.38
1971	0.58	0.59	0.59	0.59	0.57	0.50	0.54	0.46	0.63	0.75	0.85	0.92		0.25
1972	0.34	0.35	0.36	0.36	0.36	0.34	0.37	0.34	0.39	0.43	0.55	0.65	0.83	

for both large and small vessels for all years, and 4) the kill rate itself for sets with backdown did not change over the years.

Although each of the unaccounted for factors could have an effect on the estimated numbers of dolphins killed, the magnitude of such effects is probably smaller than the magnitude of the effects of vessel size, set success, and use of backdown described in this study. For example, although the kill rate data available are few, there are some additional data which are not available to us, but which are reportedly similar (Smith and Lo 1983). The last three assumptions noted above deal with the dolphin kill rates with and without backdown, and would tend to both increase and decrease the estimates, if they could be taken into account.

Our estimates of the total number of dolphins killed (Table 4) are slightly lower than previous estimates made using the same method (Smith 1979[6], 1983). The previously estimated total number of dolphins killed from 1959 to 1972 was 5.1 million (total of Smith's [1983] table 4, divided by 0.96 for other species and by 1.048 for injured animals). The difference between the two estimates resulted from the revision of the estimated number of sets that capture tuna associated with dolphins (Punsly 1983) and of the numbers of dolphins killed per set (Smith and Lo 1983).

There are alternate approaches to estimating the numbers of dolphin killed. For example, estimates could be made from data on the numbers of fishing trips made (kill-per-trip), or the number of tons of tuna caught (kill-per-ton). These approaches make different assumptions about the fishing process (Lo et al. 1982; Hammond and Tsai 1983), and require data which are not as precise as are data on the total numbers of sets. For example, fishing trips are difficult to count consistently because they may not be completed within the calendar year and may be extended by partial unloading of the catch. There are fewer such problems with the data for kill-per-set estimators on the number of dolphins killed, and the problems that exist have already been resolved (Punsley 1983).

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[6] Smith, T. D. (editor). 1979. Report of the Status of Porpoise Stocks Workshop, August 27-31, 1979, Southwest Fisheries Center, La Jolla, California. Southwest Fish. Cent., Admin. Rep. LJ-79-41, 120 p.

APPENDIX

In Equation (7), the first and second terms on the main diagonal are

$$V(\hat{R}_{\bullet t11} f_t) = V(\hat{R}_{\bullet i11})V(f_t) + \hat{R}^2_{\bullet t11} V(f_t) + f_t^2 V(\hat{R}_{\bullet t11}) \qquad \text{(A-1)}$$

for $i = 1$ and 2, noting that $\mathrm{Cov}(\hat{R}_{\bullet t11} f_t) = 0$.
The variance of f_t is given by

$$\begin{aligned} V(f_t) = {} & V(\hat{P}_t)\,(1 + V(\hat{C})) + \hat{P}_t^2\, V(\hat{C}) \\ & + \hat{C}^2\, V(\hat{P}_t) + V(\hat{C}) - 2V(\hat{P}_t)\hat{C} \\ & - 2V(\hat{C})\hat{P}_t^2 + 2\,\mathrm{Cov}(\hat{P}_t, \hat{C}). \end{aligned} \qquad \text{(A-2)}$$

This last term is assumed to be zero, as noted above. The off-diagonal element in Equation (7) is

$$\mathrm{Cov}(\hat{R}_{\bullet i11} f_t, \hat{R}_{\bullet j11} f_t) \approx \hat{R}_{\bullet i11}\, \hat{R}_{\bullet j11}\, V(f_t) \qquad \text{(A-3)}$$

for $i \neq j = 1$ and 2.

In Equation (8), based upon Equation (5)

$$\mathrm{Cov}(\hat{Q}_{ui}, \hat{Q}_{mj}) = \begin{cases} \mathrm{Cov}(\hat{R}_{\bullet i11} f_u, \hat{R}_{\bullet j11} f_m) & \text{for } i = 1,2 \\ & \text{and } j = 1,2 \\ 0 & i \neq j \quad \text{for } i = 3,4 \\ V(\hat{R}_{\bullet i2\bullet}) & i = j \quad \text{and } j = 3,4 \end{cases}$$

where $\mathrm{Cov}(\hat{R}_{\bullet i11} f_u, \hat{R}_{\bullet j11} f_m)$ (A-4)

$$= \begin{cases} [\hat{R}^2_{\bullet i11} + V(\hat{R}_{\bullet j11})]\mathrm{Cov}(f_u, f_m) + f_u f_m V(\hat{R}_{\bullet i11}) & i = j \\ \hat{R}_{\bullet i11}\hat{R}_{\bullet j11}\, \mathrm{Cov}(f_u, f_m) & i \neq j \end{cases}$$

assuming $\mathrm{Cov}(\hat{R}_{\bullet i11}, \hat{R}_{\bullet j11}) = 0$

$$\text{and } \mathrm{Cov}(f_u, f_m) \approx \mathrm{Cov}(\hat{P}_u, \hat{P}_m)\,[V(\hat{C}) + \hat{C}^2] + V(\hat{C}) \bullet [1 + \hat{P}_u \hat{P}_m - \hat{P}_u - \hat{P}_m]. \qquad \text{(A-5)}$$

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FECUNDIDAD PARCIAL DE LA SARDINA PERUANA (*SARDINOPS SAGAX*)

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RESUMEN

La fecundidad parcial promedio de sardina peruana (*Sardinops sagax*) de una colección de 91 peces de Chimbote, Perú, en setiembre-octubre 1982 fue de 55,000 (error standard = 140) y la fecundidad relativa (número de ovocitos hidratados por gramo de peso de la hembra) fue de 300 (error standard = 40). La relación entre la fecundidad parcial y el peso del pez puede ser expresada por una función lineal. Para estimar la fecundidad parcial, se recomienda tomar tres submuestras de diferentes posiciones del más grande de los dos ovarios porque se encontró que las densidades de los ovocitos hidratados dentro del ovario fueron diferentes. Se ha comparado la estimación de algunos parámetros relacionados a la fecundidad parcial entre sardina peruana y anchoveta del norte (*Engraulis mordax*).

ABSTRACT

The average batch fecundity of Peruvian sardine (Sardinops sagax) from a collection of 91 fish off Chimbote, Peru, in September-October 1982 was 55,000 (se = 140) and the relative fecundity (number of hydrated oocytes per gram female weight) was 300 (se = 40). The batch fecundity and fish weight relationship can be expressed by a linear function. We recommended three subsamples taken at different locations from the larger of the two ovaries for estimating the batch fecundity because the egg densities were found to be different within the ovary. Estimates of some parameters related to batch fecundity were compared between Peruvian sardine and northern anchovy (Engraulis mordax).

INTRODUCCION

Normalmente se estima la fecundidad parcial de un pez contando los huevos en submuestras de tejido ovárico porque se perdería demasiado tiempo en contar todos los huevos que se encuentran dentro del ovario (Hunter et al. 1984). Se ha investigado muchos aspectos de la fecundidad parcial de la anchoveta del norte (Engraulis mordax) (Hunter y Goldberg 1980, Hunter y Macewicz 1980, Hunter et al. 1984) y la fecundidad parcial de sardina del Pacífico (Sardinops caerulea) fue estimada por MacGregor (1957). En este trabajo, para estimar la fecundidad parcial de la sardina peruana (Sardinops sagax) hemos seguido el procedimiento desarrollado para estimar la fecundidad parcial de anchoveta del norte. Se ha examinado estadísticamente los conteos de ovocitos hidratados de submuestras de ovarios de sardina y el efecto de localización y número de estas submuestras sobre la estimación de la fecundidad parcial de la sardina peruana. También examinamos la relación funcional entre la fecundidad parcial y el peso del pez porque los peces más grandes llevan más huevos. Finalmente hemos comparado algunos parámetros relacionados a la estimación de la fecundidad parcial entre sardina peruana y anchoveta del norte.

MATERIAL Y METODOS

Las sardinas procedieron de bolicheras comerciales de Chimbote, Perú, entre setiembre y octubre 1982. Para estimar la fecundidad de sardina, se usó el estado de predesove, cuando los ovarios están hidratados (Hunter y Goldberg 1980). Enseguida de sacar las sardinas de la bolichera, se abrió la cavidad del cuerpo desde el ano hasta las aletas pectorales y los ovarios se preservaron en solución de formalina buferada (Hunter _et_ _al_. 1984).

Para determinar la fecundidad parcial se siguió el procedimiento descrito por Hunter _et_ _al_. (1984). En el laboratorio, se secó el ovario con papel filtro y se pesó lo más próximo a 10 mg. Tres submuestras se tomaron del ovario más grande. Sus posiciones fueron: distal-dorsal (superficial), central (interior), apical-ventral (superficial) (Fig. 1). En 60 hembras se tomaron también tres submuestras del ovario más pequeño.

Las tres submuestras sacadas del tejido ovárico tuvieron un peso aproximado de 100 mg. Cada submuestra fue extendida sobre una lámina porta-objetos y se le agregó una gota de glicerina. Se contó el número de ovocitos hidratados en cada submuestra.

Para determinar la fecundidad parcial, se calculó el número de ovocitos hidratados por gramo de submuestra y luego se multiplicó por el peso total del ovario. la fecundidad parcial por hembra fue calculada como el promedio derivado de estas submuestras.

Posición de las submuestras dentro del ovario

Las submuestras pueden ser tomadas tanto del ovario derecho como del izquierdo, de la parte superficial o interna, y de la parte posterior o anterior del ovario. Para estandarizar el procedimiento es importante fijar la posición de las submuestras. Para determinar los efectos de la posición de las submuestras dentro del ovario, en la estimación de la fecundidad parcial, analizamos los conteos de ovocitos hidratados de seis submuestras ováricas (tres de cada ovario) de 60 peces. Las tres posiciones usadas son distal-dorsal (superficial), central (interior) y apical-ventral (superficial). Para cada submuestra de tejido, se obtuvo el número de ovocitos hidratados por gramo de ovario (y/z) (y = número de ovocitos hidratados y z = peso de la submuestra). Se realizó análisis de varianza (dos ovarios y tres posiciones) con los números de ovocitos hidratados por gramo de ovario (Tabla 1). El análisis indicó que la diferencia entre las densidades de ovocitos hidratados de los dos ovarios no fue detectable. Sin embargo, las densidades de ovocitos hidratados de las tres posiciones no fueron las mismas: la densidad de los ovocitos hidratados de la posición distal-dorsal fue siempre menor que las otras dos posiciones. La menor densidad de ovocitos hidratados por unidad de peso en la posición posterior (distal-dorsal) fue probablemente causada por la hidratación avanzada de los ovocitos en esta parte del ovario. En anchovetas y sardinas, la hidratación de los ovocitos que van a ser desovados en la noche, comienza en la mañana del mismo día y continúa hasta el desove. Mientras que este proceso parece ocurrir con la misma velocidad en todas las partes del ovario de anchoveta, en la sardina parece avanzar en forma desigual en las diferentes partes del ovario. También se notó que la varianza de la densidad de los ovocitos hidratados dentro del ovario fue homogénea entre ovarios.

Número óptimo de submuestras (m)

El número óptimo de submuestras fue determinado de acuerdo al procedimiento desarrollado para la fecundidad parcial de anchoveta del norte (Lo Ms, Hunter *et al*. 1984). Basado en un modelo de efectos aleatorios (Scheffé 1959), el número óptimo de submuestras fue definido como el que produce la mejor estimación de la varianza (σ_A^2) asociada con el modelo. Este modelo está ajustado a la fecundidad parcial (Y) y al peso del pez (X), cuando se han contado todos los ovocitos hidratados. El modelo general puede ser descrito como Y = f (X) + a, donde a es el término de error con promedio = 0 y varianza = σ_A^2. Cuando el número de los ovocitos hidratados es estimado en base de m submuestras (denotado por Y), el modelo f (X) es ajustado a los datos (Y, X). La varianza (σ_{ε}^2) asociada al modelo ajustado a los datos (Y, X), tiene dos fuentes la desviación de Y respecto del valor de f (X), σ_A^2, y la desviación de $\hat{Y}$ de Y, σ_e^2, en la forma de $\sigma_e^2 = \sigma_A^2 + \sigma_e^2/m$. La varianza ($\sigma_{\varepsilon}^2$) puede ser estimada por medio de un análisis de regresión. La varianza (σ_e^2) puede ser estimada de las unidades de las submuestras. La estimación de σ_A^2 (s_A^2) puede ser obtenida por sustracción: $_A^2 = s^2 - s_e^2/m$. El principal parámetro estadístico para el cómputo del número óptimo de submuestras es $\Theta = s_e^2/s_A^2$. Para la sardina peruana, $\Theta = 0.35$ (Tabla 2). Según Lo (Ms), si $\Theta < 0.5$, el número óptimo de submuestras dentro del ovario es 2. Entonces la varianza asociada con el modelo que está ajustado a la fecundidad parcial estimada de dos submuestras es, en promedio, 1.2 veces la varianza del mdoelo cuando son contados todos los ovocitos hidratados (Hunter *et al*. 1984). El número óptimo de submuestras para otros valores de Θ son indicados en Lo (Ms) y Hunter *et al*. (1984).

Relación funcional entre la fecundidad parcial y el peso del pez sin ovario

La fecundidad parcial (Y) de un pez varía con su peso (X). Es necesario la selección de un modelo apropiado para describir la relación entre la fecundidad parcial y el peso del pez. Para determinar esta relación, hemos agregado 31 peces más a la colección original de 60 ejemplares. Para cada uno de los 91 peces se usaron tres submuestras tomadas del ovario más grande y la estimación de la fecundidad parcial (Y) se computó como el número promedio de ovocitos hidratados por gramo de ovario (y/z) de las submuestras, multiplicado por el peso total (Z) del ovario ($Y = Z\,(\Sigma(y/z)/3)$. Se ajustaron 5 modelos a los datos de sardina (Y, X) (Tabla 3). Entre estos 5 modelos $Y = a + b/n\,(X)$ tuvo el promedio más bajo. Los 5 mínimos cuadrados no fueron estadísticamente diferentes.

DISCUSION

Como se ha detectado una diferencia significativa entre las densidades de los ovocitos hidratados del ovario derecho e izquierdo, las submuestras pueden ser tomadas de cualquier lado. El número mínimo de submuestras de un ovario debería ser de dos. Por conveniencia se recomienda tomar tres submuestras porque el el tiempo que se necesita para procesar una submuestra adicional es alrededor de 10-15 minutos. Sin embargo, si los costos de procesamiento de las submuestras son altos, una sola submuestra por hembra tomada de la parte cental del más grande de los dos ovarios debe ser suficiente, porque la varianza en la estimación de la fecundidad parcial dentro de las submuestras es pequeña comparada con la varianza de la fecundidad parcial asociada con el modelo (Fig. 2, Tabla 2).

La fecundidad parcial de la anchoveta del norte fue estimada primeramente en 1950 (MacGregor 1968) y para cada año desde 1978. La fecundidad parcial por gramo de hembra de anchoveta varió entre años. El promedio (1978-83) de la fecundidad relativa (fecundidad parcial por gramo de hembra) es 614 (error standard = 0.19) y la fecundidad parcial es 8,435 (error standard = 213). La fecundidad relativa de sardina es 283 (error standard = 40) y el promedio de la fecundidad parcial es 54,567 (error standard = 136). El tamaño promedio de sardinas hembras (160 grs) muestreadas frente al Perú fue más grande que las anchovetas hembras (15 grs) muestreadas en California ya que la fecundidad relativa de las sardinas fue sólo la mitad que la fecundidad de las anchovetas (Tabla 4). La posición de las submuestras usadas para estimar la fecundidad parcial no es tan importante para las anchovetas como para las sardinas posiblemente debido también a la heterogeneidad en la hidratación. En sardinas, la densidad de los huevos de la posición posterior del ovario parece ser siempre menor que en otras partes del ovario. Las densidades de los huevos del ovario derecho e izquierdo fueron similares para ambas, sardina y anchoveta.

La relación entre fecundidad parcial y el peso de la hembra (sin ovario) puede ser expresada por una función lineal para ambas, anchoveta y sardina. Para la anchoveta del norte anteriormente se usó un modelo exponencial y un modelo lineal. Ahora se aplica el lineal. Para una comparación directa de estas dos especies, se escogió el modelo lineal porque el coeficiente de regresión es la fecundidad parcial por gramo de hembra.

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TABLA 1. Análisis de varianza de dos vías para verificar el efecto de la posición de la submuestra en el ovario de la sardina, sobre el número de huevos hidratados por gramo de ovario, en base a los datos tomados de 60 hembras. Las tres posiciones son I = distal-dorsal (superficie), II = central (interior), y III = apical-central (superficie) para el ovario derecho (R) y el izquierdo (L).

Número promedio de huevos por gramo de ovario

		Posiciones			
		I	II	III	TOTAL
	y/z	2055	2265	2310	2210
R	s	349	380	445	407
	n	60	60	60	180
	y/z	2060	2366	2324	2250
L	s	359	400	343	391
	n	60	60	60	180
	y/z	2058	2316	2317	2230
TOTAL	s	352	392	396	399
	n	120	120	120	360

Análisis de varianza de dos vías del número de huevos por gramo de ovario

SS debido a	D.F.	SS	MS	F
Derecho versus Izquierdo	1	145563	145563	1
Posición dentro del Ovario	2	5352096	2676048	18.45
Interacción	2	169191	84596	0.58
Error	354	51355044	145071	
Total	359	57021891		

TABLA 2. Estimación del parámetro $\theta = \sigma_e^2/\sigma_A^2$ para la determinación del número óptimo de submuestras dentro del ovario. Un modelo lineal (Y = 5514 + 281X) fue usado el que está basado en 60 sardinas peruanas (n = 60) con seis submuestras.

Fuente de Variación	Fórmula	Estimación
Dentro del Ovario: (s_e^2)	$\dfrac{\sum_{i=1}^{60} \sum_{j=1}^{6} (Y_{ij} - Y)^2}{60\,(6 - 1)}$	25 450 500
Valor Residual de $\hat{Y} = f(X) + \xi$: (s^2)	$\dfrac{\text{Sumas Residuales de Cuadrados}}{(60 - 2)}$	75 973 952
Valor Residual de $Y = f(X) + a$: (s_A^2)	$s^2 = s_e^2/6$	71 732 202
Coeficiente de Varianza:	s_e^2/s_A^2	35

TABLA 3. Cinco modelos usados para expresar la relación entre la fecundidad parcial de la sardina (y) y el peso de la hembra (sin ovario) (x), en base a 91 hembras con tres submuestras.

	PARAMETROS				
MODELO	a (se)	b (se)	c (se)	MSE(s_ε^2) X 10^{-7}	r^2
$y=a+bx$	9435 (5801)	283 (36)		9.986	0.41
$y=ax^b$	851 (452)	0.82 (0.10)		9.943	
$y=ae^{bx}$	25361 (2064)	0.005 (.0006)		10.281	
$y=a(b/a)^{e^{-c(x-100)}}$	82145 (16576)	33586 (4350)	0.014 (0.007)	9.894	
$y=a+b\ln(x)$	-179523 (29012)	46300 (5735)		9.817	0.42

TABLA 4. Parametros relacionados a la fecundidad parcial de la sardina peruana y la anchoveta del norte (x = promedio, SE = error estandard).

	Sardina peruana			Anchoveta del norte (1978-83)		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Peso de Hembra (g) (sin ovario)	160	3	91	15	0.28	419
Peso del Ovario (g)	28	0.93	91	3	0.07	419
Regresión de la Fecundidad relativa	283	36	91	614	0.19	419
Mejor Modelo :	Y=a+bln(x)			y=a+bx		

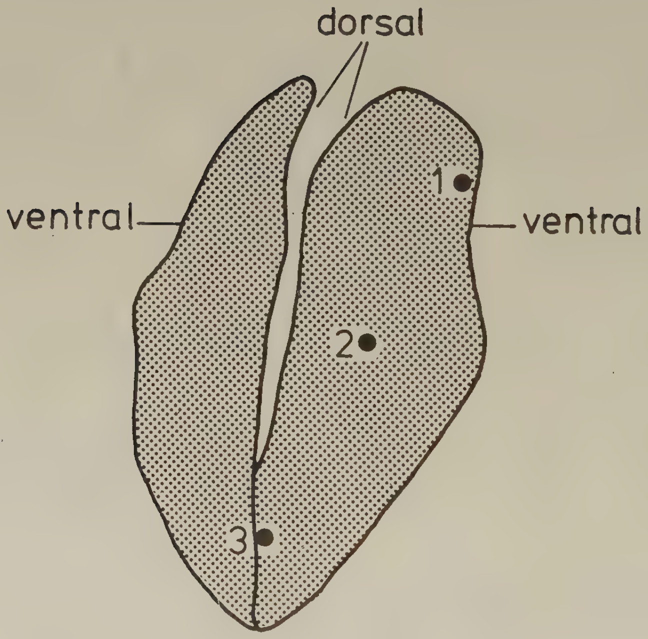
dorsal
ventral
ventral
1
2
3

Figura 1. Posiciones de las tres submuestras tomadas del ovario de la sardina peruana. 1. apical-ventral (superficie), 2. central (interior), 3. distal-dorsal (superficie).

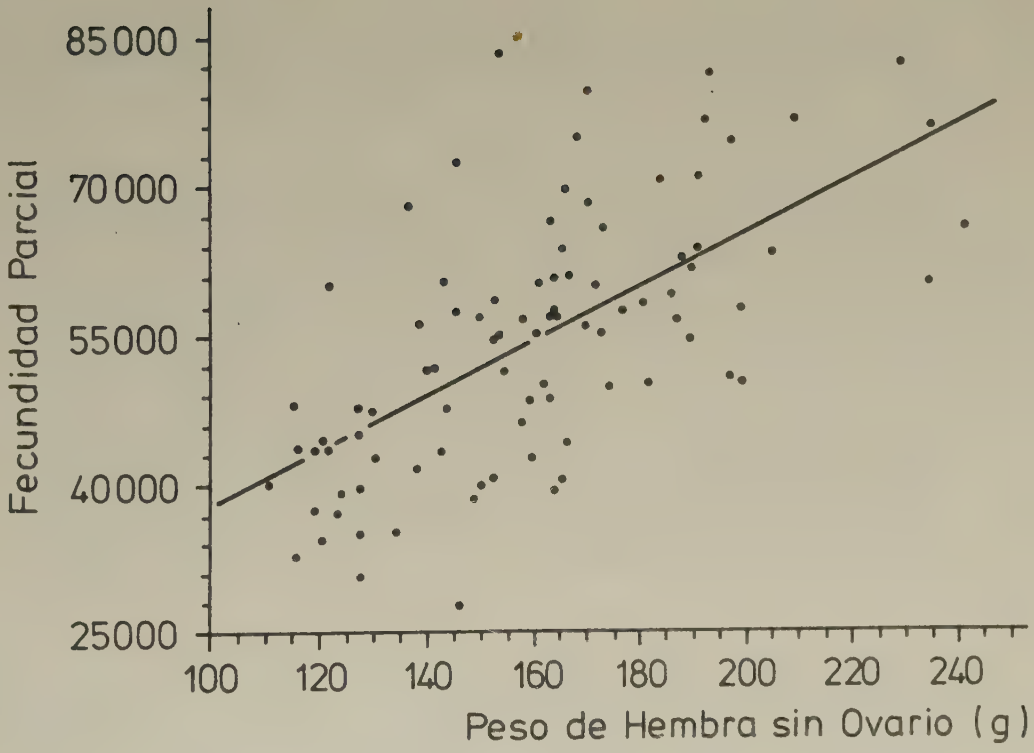

Figura 2. Diagrama de puntos de la fecundidad parcial y del peso de hembra (sin ovario) y un modelo ajustado a los datos (y = a + bx).

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The Subarctic and Northern Subtropical Fronts in the Eastern North Pacific Ocean in Spring

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ABSTRACT

The subarctic and subtropical frontal zones of the eastern North Pacific Ocean were surveyed in June for five consecutive years starting in 1972. These surveys form the basis for a description of the complex frontal distributions and their year-to-year differences. The fronts appear as surface outcroppings of haloclines: the subarctic halocline where salinity increases with depth and the subtropical halocline where the opposite prevails. Between the fronts lies a transition zone where strong vertical gradients of salinity are generally absent. An examination of the northern boundary of subtropical waters in this new dataset reveals the presence of two major fronts in the subtropical frontal zone. In addition to the front commonly identified as the subtropical front (18°C and 34.8‰) is a northern subtropical front that forms the northern boundary of the subtropical halocline in the eastern North Pacific. It falls some 2° to 3° of latitude north of the subtropical front and is the same front observed by Roden which he termed the "34°N front". There is evidence that this front is quasi-continuous over great distances like the other major fronts of the temperate zone. Its temperature–salinity characteristics, 14° to 17°C and 34.4 to 34.6‰, are also those of Kuroshio front in the Kuroshio Extension. Narrow cores of extra-high salinity that indicate current jets occur at the high-salinity side of the northern subtropical front and, sometimes, the subarctic front. Geostrophic flow is often locally intensified about the fronts. The many salinity features are closely associated with the velocity patterns, indicating the complexity of advection and suggesting, at times, a banded structure in the current field. In June 1972, 1973 and 1976 the frontal gradients were strongly developed; in June 1974 they were diffused and broken. These findings agree with Saur's time-series study of surface salinity gradients along a track crossing the same area and concurrent in time.

1. Introduction

This study examines a series of five surveys that were conducted during June of consecutive years, starting in 1972. Meridional transects from each of the surveys cross both fronts bounding the subarctic and subtropical waters in the eastern North Pacific Ocean and one such line of stations along 137.5°W was repeated in each of five years. These surveys provide the basis for describing details of the complex frontal structure during a season and in a region that has not been studied previously, and provide some evidence of the year-to-year differences in frontal development. The fronts found in these observations are the subarctic, the subtropical and a front, herein called the northern subtropical, which lies between them.

Within the past one-and-one-half decades the use of conductivity (salinity)/temperature/depth (CTD or STD) profilers has improved the observation of ocean frontal gradients. The subarctic and subtropical frontal zones in the eastern North Pacific Ocean have been studied by Roden (1971, 1974, 1977, 1980) in four surveys, using a CTD and relatively small station intervals (27 to 36 km). His surveys centered about the months of September, October, November and January. Recently, there was a cooperative investigation of the subtropical front in the month of January, FRONTS 80 (Paulson and Niiler, 1981; Roden, 1981; Van Woert, 1982; Niiler and Reynolds, 1984). The primary characteristics of these frontal zones and processes that influence them are reviewed and summarized by Roden (1975, 1980) and by Niiler and Reynolds (1984).

The time variation of these fronts has been examined by Saur (1980) in a study of the surface salinity observations taken approximately biweekly over nine years (1965–75) along the shipping lane between San Francisco and Honolulu. The surveys reported herein were conducted within the period of Saur's record of observations and the station tracks intersect his transect near the subtropical frontal zone. A comparison is made between Saur's time series of fronts as determined by surface salinity and the new observations of detailed hydrographic sections taken once each year. Each oceanographic transect of this new dataset crosses the fronts near the eastern terminus of their zonal extent and the distribution appears to reflect the deep-mixed winter conditions even though they are overlain by shallow spring warming.

2. Background

Large meridional differences in the balances of heat exchange through the surface and of evaporation and precipitation produce meridional variations in temperature and salinity characteristics. Large-scale patterns of wind stress and ocean currents form these meridional gradients into relatively narrow zones, thus producing ocean fronts (Roden, 1980). These fronts sometimes reach depths on the order of several hundred meters and act to separate large regions having small ranges of temperature–salinity characteristics, termed water masses. The primary characteristics used in defining the subarctic region are its low temperatures and low salinities (<33.8‰) in the surface domain and a halocline near 150 m in which salinity increases with depth. The southern limit of this ocean region is the subarctic front. It is defined by the abrupt meridional change in salinity structure (e.g., see Favorite et al., 1976, and ref. cited therein). Dodimead (1961) and Tully and Barber (1960) used the 33.8‰ isohaline to characterize this front; it falls near the bottom of the subarctic halocline and rises to the surface within the subarctic front. The subarctic front retains its characteristic structure from the western North Pacific to regions off California and Baja California (Roden, 1971; Lynn et al., 1982). The front generally lies between latitudes 40° and 43°N except to the east of 150°W where it turns east-southeast forming a western boundary for the California Current and where LaFond and LaFond (1971) and Saur (1980) use the term "California Front". In either case the argument is drawn that the salinity structure gives credibility to the existence of the subarctic front as a quasi-permanent and quasi-continuous feature and that it closely follows the mean position of 33.8‰ waters in the surface domain. This concept appears valid despite deformations and temporal variations that sometimes give it a complex form. There are additional ocean fronts in the subarctic waters (Roden, 1977), some of which are revealed in the figures herein; however, they are not treated in this report.

The North Pacific Central Waters (Sverdrup, 1942) are characterized at the surface by salinities in excess of 34.8‰ and a halocline (and associated thermocline) often in a depth range of 100 to 250 m in which salinity decreases with depth. The northern boundary of North Pacific Central Waters is the subtropical front in which the 34.8‰ isohaline and the 18°C winter isotherm are embedded (Seckel, 1968; Roden, 1980). During FRONTS 80 (Roden, 1981) one manifestation of this front was comprised of salinities in the range of 34.9 to 35.1‰. Although the subtropical front has been observed less often than the subarctic front, it appears as if the mean position of the 34.8‰ (or perhaps 34.9‰) isohaline at or near the surface (e.g., from Robinson, 1976) serves the same function in defining the average position of the subtropical front for the greater part of the North Pacific. The central latitude of this front is 30.5°N. Roden (1975) presented a schematic representation of the major fronts in the North Pacific. Like the subarctic frontal zone the subtropical frontal zone has multiple regions of large gradients. Between meridians 152 and 158°W, in a winter survey, Roden (1980) found the subtropical front near 31.5°N and a second front near 34°N. He termed the more northerly front the "34°N front". The 34.4 and 34.5‰ isohalines and the 16°C isotherm are embedded in it.

One of the fronts described in this report is an eastward continuation of the "34°N front". Like the other two major midlatitude fronts this front is found at more southerly latitudes nearer the North American continent. Because of this variation in latitude, the name "34°N front" appears inappropriate; hereafter, I refer to it as the northern subtropical front. Evidence for this front can be found in these and other data and I conclude that it is a major feature of the subtropical frontal zone, not only in the eastern North Pacific, but in the central and western North Pacific as well. The evidence for the possible continuity of this front is given in Section 9. In the eastern North Pacific it falls some 2 to 3 degrees of latitude north of the subtropical front and is shown schematically in Fig. 1.

3. The surveys

Surveys were conducted each June of the years 1972 through 1976. The station lines for the surveys are shown in Fig. 1, along with the fronts for two of the years as determined from these and other data. The common element in each of the survey tracks is the repetition of the hydrographic section along 137°30′W. In 1972 and 1975 operations were conducted from the R.V. *Townsend Cromwell*. In 1973, 1974 and 1976 the R.V. *David Starr Jordan* was used. For the purposes of this paper the surveys may be identified in sequence as TC72, DSJ73, DSJ74, TC75 and DSJ76.

Station observations include STD (Plessey Inc., model 9006 or 9040) casts to 600 or 1000 meters. Nansen bottles or a rosette sampler attached to the STD cable provided water samples and reversing-thermometer temperatures for standardization of the STD casts, as did occasional 18-bottle Nansen casts. Stations were frequently spaced at 45 to 56 km (25 to 30 n. mi.) along the transects. Stations were added in response to locating the fronts with the continuous recording thermosalinograph. In addition to the major transects, short runs were made across the frontal features with 9 and 19 km (5 and 10 n. mi.) station spacing.

The surveys were conducted as part of study of albacore migration patterns as they enter the North

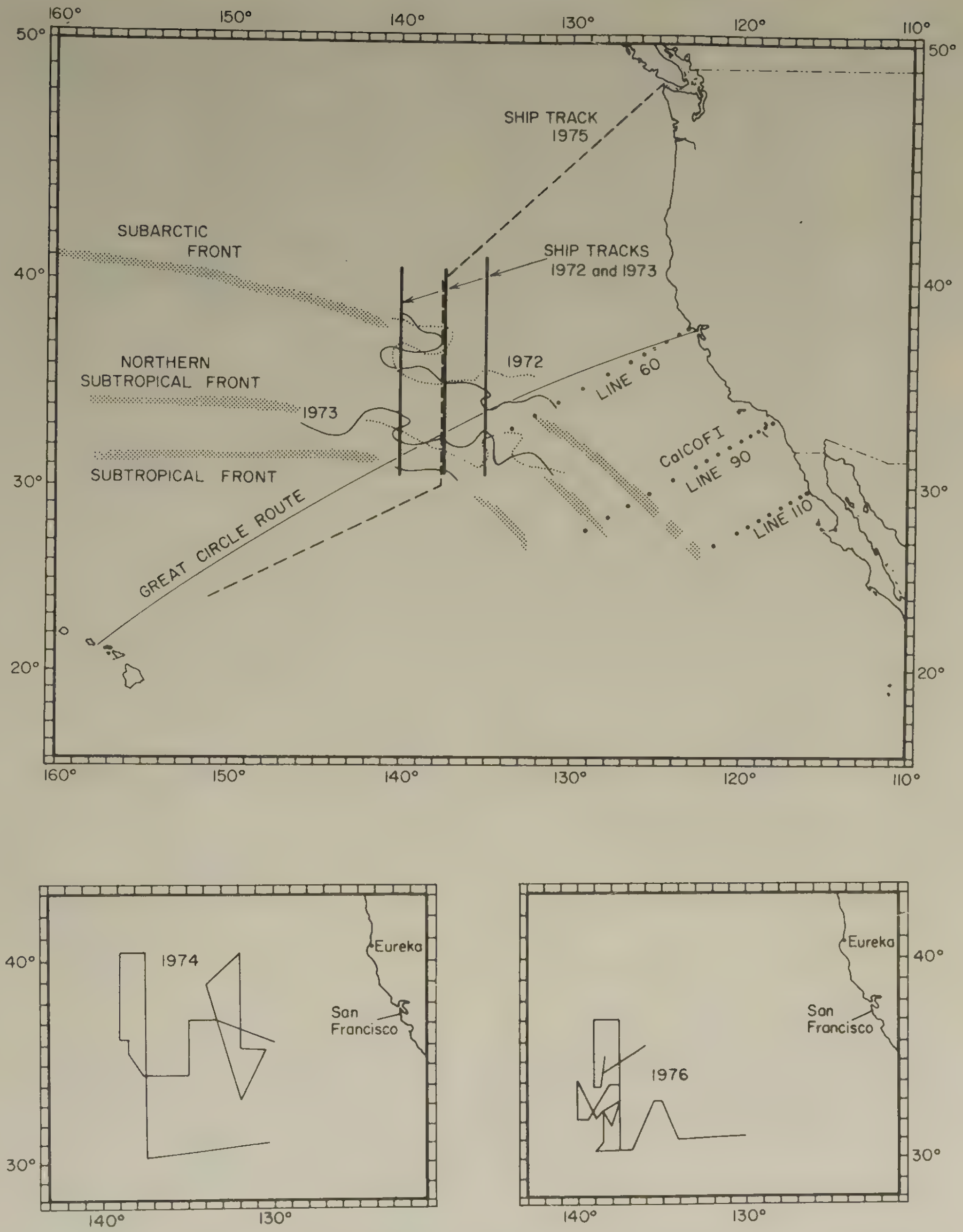
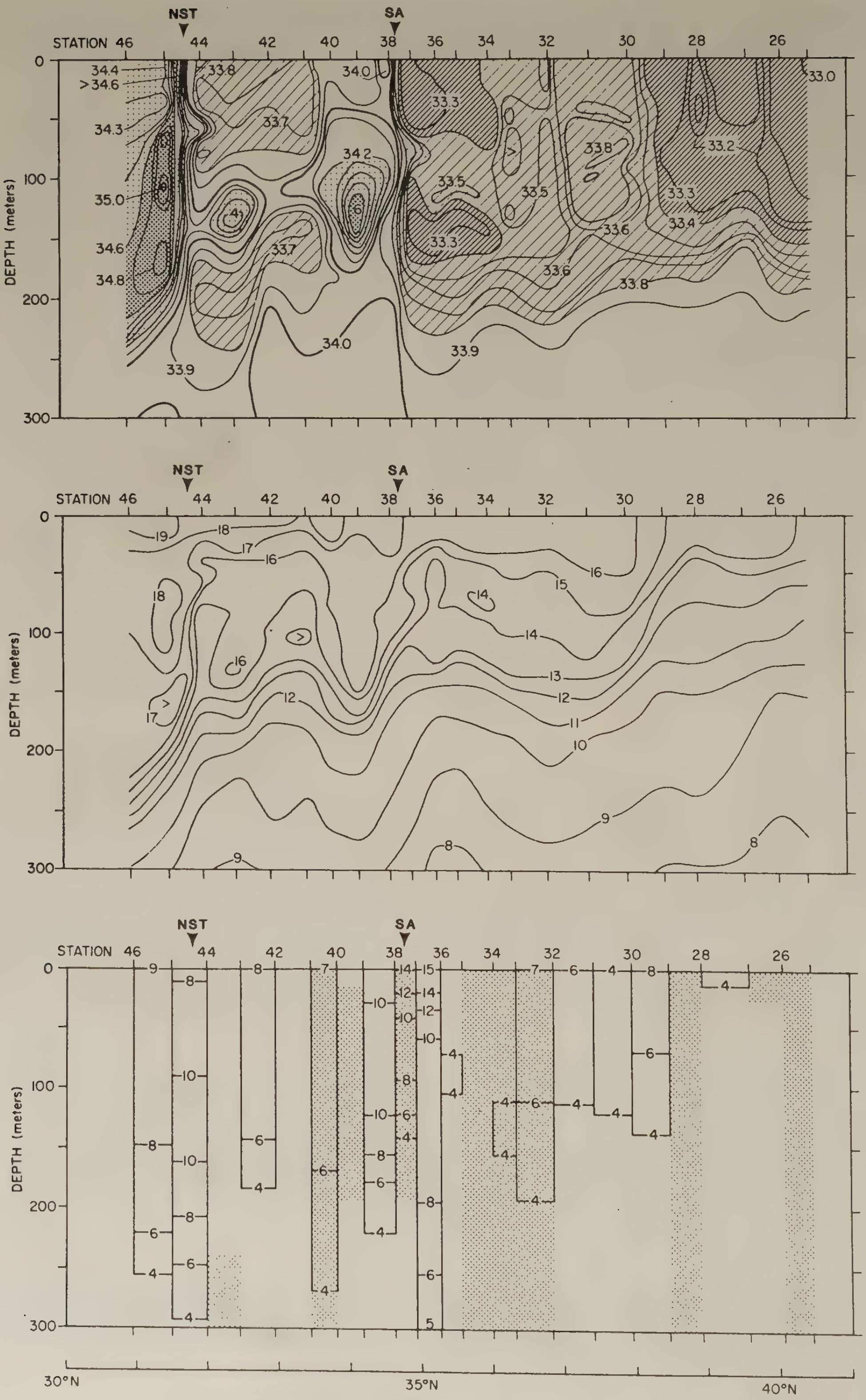

SHIP TRACK
1975
SUBARCTIC
FRONT
SHIP TRACKS
1972 and 1973
NORTHERN
SUBTROPICAL FRONT
1972
1973
LINE 60
CalCOFI
LINE 90
SUBTROPICAL FRONT
LINE 110
GREAT CIRCLE ROUTE
160°
150°
140°
130°
120°
110°
50°
40°
30°
20°
1974
Eureka
San
Francisco
1976

FIG. 1. Upper: Schematic of station lines occupied in June of 1972, 1973 and 1975 (heavy solid and dashed lines). Great-circle shipping route between San Francisco and Honolulu along which time series of surface salinity were analyzed by Saur (1980) (light line). Mean position of the subarctic and subtropical fronts (shading) and observed fronts for 1972 and 1973 (dotted and light solid line). Three often-repeated station lines from the CalCOFI station grid are shown. Lower: Schematic of station lines occupied in June of 1974 and 1976.

American west coast fishery in late spring to early summer (Laurs and Lynn, 1977). Fishing vessels chartered by the American Fishermen's Research Foundation cooperated in these surveys. Twice-daily XBT drops by these vessels and XBT drops from the Merchant Ship XBT program coordinated by J. F. T. Saur and


NST
SA
STATION 46 44 42 40 38 36 34 32 30 28 26
DEPTH (meters)
0
100
200
300
34.4
>34.6
34.3
35.0
34.6
34.8
33.8
33.7
34.0
34.2
33.3
33.5
33.6
33.2
33.4
33.0
33.9
19
18
17
16
15
14
13
12
11
10
9
8
30°N
35°N
40°N

D. R. McLain provided additional data to extend the determination of the fronts for 1972 and 1973 in Fig. 1 beyond the research vessel tracks.

4. Distributions of June 1972 and June 1973

a. *Salinity frontal structure*

Of three meridional transects occupied in both June 1972 and June 1973 the central one, along 137°30′W, was chosen to show the salinity structure (Figs. 2 and 3). Both the subarctic and northern subtropical front form a geographic limit to their respective haloclines. The intervening waters of the transition zone show intermediate values of salinity varying about 34.0‰ and lack a horizontally continuous halocline. Waters on both sides of both fronts exhibit complicated structure including isolated pockets and layers of salinity extremes. Some of these features in the salinity structure are found to occur in some form or other in each or most of the vertical sections for the 5-year data series and hence apparently are structurally a part of the front and indicative of some complex scheme of frontal dynamics. They are described in the following in some detail. It should be noted that the STD-derived salinity contours of these and other figures were drawn to conform, as well, to the record of surface salinity recorded continuously along each track by the thermosalinograph.

There is a zonal band of water immediately south of the northern subtropical front that has higher salinity than waters to the north or south. Approaching from the north, the salinity shows an abrupt increase southward across the front, where it reaches a maximum, and then decreases away from the front to a minimum before increasing again at the subtropical front. This pattern of horizontal variation occurs throughout the upper 300 m including levels below the subtropical halocline. Within this band of high-salinity water the maximum salinity in the water column is found at intermediate levels, 70 to 150 m. In Figs. 2 and 3, the cross-sectional area of waters exceeding 34.8‰ within the subsurface maximum is small, but such waters also occur in the transects occupied to the east and west of those shown. This distribution appears as a core or multiple cores of high-salinity water that follow the south wall of the front.

There is a zonal band of water just north of the subarctic front in which salinities are a local minimum, appearing somewhat in mirrored contrast to the band of high salinity south of the northern subtropical front. Between the surface and 200 m salinities decrease northward through the subarctic front, reach a minimum, and increase slightly for a degree or so of latitude before decreasing farther north. The lowest-valued contours in this band are subsurface and form two diffuse cores separated by a layer of weakly defined salinity maximum. One result of the overall salinity pattern is that the lateral salinity gradients across the fronts are greater below the surface. Both the northern subtropical and subarctic fronts in the TC72 section along 137°30′W (Fig. 2) exhibited the largest station-to-station differences observed, exceeding 1.1‰ over 54 km at various intermediate levels within the upper 200 m of the northern subtropical front and 0.8‰ over 33 km at the subarctic front.

There are two relatively shallow layers where salinity is an extreme that are evident in all the transects. A layer where salinity is a maximum occurs near 140 m which is most evident where it projects northward from the northern subtropical front (Figs. 2 and 3). Kenyon (1978) noted this feature in his zonal section along 35°N. Kenyon's section may be entirely within the transition zone where it shows the shallow maximum to occur only between 133° and 142°W. A layer of minimum salinity, at 150 to 230 m, projects southward from the base of the subarctic front and often extends beneath the subtropical halocline. Although this minimum is continuous over most of the extent of these transects the values vary with latitude producing many closed contours. This salinity minimum extends over much of the eastern North Pacific (Reid, 1973; Tsuchiya, 1982).

The STD transects of TC72 did not extend across the subtropical front. In the 1973 survey one station fell south of this front at 137°30′W (Fig. 3) as did several along 140°W. Salinities exceed 35.0 or 35.1‰ on the southern side.

b. *Thermal structure*

Horizontal temperature gradients are coincident with the frontal salinity gradients. At the sea surface the gradient can be about 0.2°C km^{-1} with a total difference across the front being a modest 0.5 to 1.5°C. Below the seasonal thermocline the fronts appear as abrupt changes in depth of isotherms (Figs. 2 and 3). There are usually one or two isotherms (in unit °C) which are central to the large subsurface salinity gradients and which show the largest displacement in depth across each front. The 16 and 17°C isotherms are central to the northern subtropical front. The 14 and 15°C isotherms are likewise associated with the largest salinity gradients in the subarctic front. The same isotherms are associated in the same manner with the fronts in each of the sections for the other longitudes

FIG. 2. Vertical sections of salinity (‰), temperature (°C) and geostrophic velocity (cm s^{-1}) from cruise TC72 (June 1972) along 137°30′W. Only the upper 300 m is shown. Reference level for velocity is 500 db. Shaded flow is westward. Station spacing, although variable, is commonly 56 or 28 km; vertical exaggeration 1853. In this and other figures ST: subtropical front, NST: northern subtropical front and SA: subarctic front.

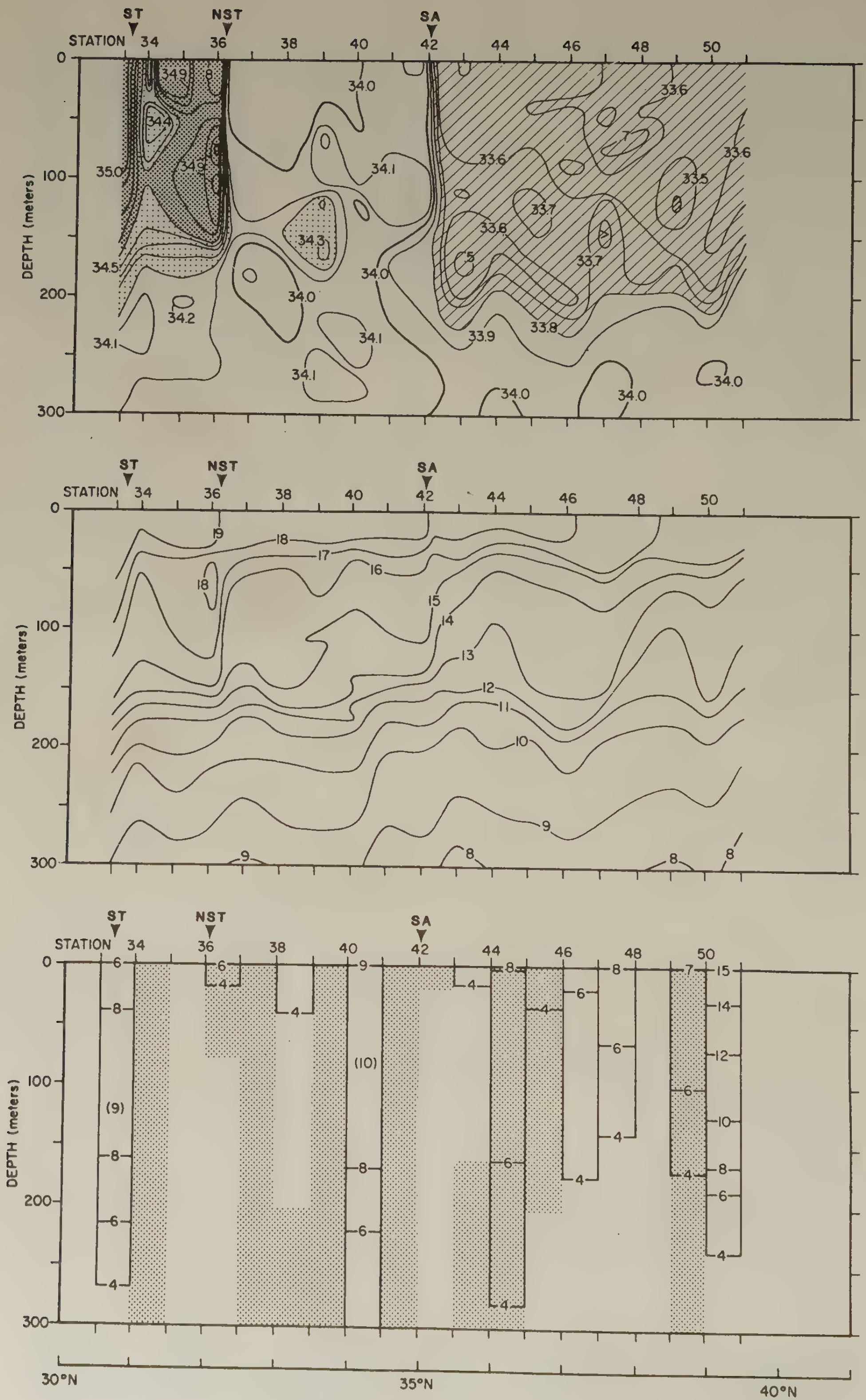


FIG. 3. Vertical sections of salinity, temperature and geostrophic velocity from cruise DSJ73 along 137°30′W.

and for the other years. The greatest subsurface horizontal temperature differences across the fronts are on the order of 2 to 3.5°C station-to-station, occurring at the same levels as the large subsurface salinity gradients. Temperature inversions appear in each domain above the haloclines and are salinity compensated.

c. *Geostrophic velocity sections*

During June 1972, geostrophic flow, primarily directed eastward, was concentrated about both fronts (Fig. 2; westward flow is shaded). Geostrophic velocities, computed for a reference level of 500 db, reached values of 10 to 14 cm s^{-1} about both the subarctic and northern subtropical fronts. Away from the fronts flow is generally weak or negligible. The higher velocities about the fronts extend to depths well below the halocline.

In contrast, velocities were negligible about the northern and central fronts along 137°30′W during June 1973 (Fig. 3). At these same fronts along 135° and 140°W flows were 6 to 7 cm s^{-1}. Higher velocities, 15 and 16 cm s^{-1} eastward, occurred on the southern side of the subtropical front 31°N, 140°W.

d. *Maps of ocean characteristics*

Maps of the distributions of surface salinity, temperature and dynamic height for TC72 are given in Fig. 4. The two fronts are shown clearly in the surface gradients of salinity (Fig. 4). (Between-station detail was provided by the trace from the continuous recording salinograph). The surface salinity gradients of the subtropical front fell outside the southwest corner of the station grid but were recorded in transit by the thermosalinograph. The subarctic front lies nearly zonally at 35°N between 140° and 137°30′W but loses definition at 135°W. The northern subtropical front has a southward loop in the midst of the survey and lies between 31° and 33°N. A meander, wavelength 180 km and amplitude 55 km, was found in the subtropical front during FRONTS 80 (Roden, 1981; Van Woert, 1982). The meander depicted in Fig. 8 has roughly twice the wavelength and amplitude. The outcropping of high-salinity cores appears at the southern edge of each front. The surface temperature for TC72 (Fig. 4, center) shows a related pattern, with higher temperatures associated with higher salinities and vice versa.

Both surface temperature and salinity fields resemble the topography of geopotential anomaly, 0/500 db (Fig. 4, right). Flow is faster near the fronts where the gradient of geopotential anomaly is greater. Here the flow is largely eastward (indicated by arrowheads). The tongues of relatively high and low salinity near 37°N are each centered in a flow pattern that would explain their presence by advection. Westward flow in the southwest corner may provide the waters with the characteristic dropoff in salinity from the peak values south of the northern subtropical front. Roden (1980) concluded from his observations that during winter (January), geostrophic flow and temperature and salinity fields show no association at the sea surface but have a strong association at 150 m. In these data, the association extends to the surface.

The layers of salinity extremes lie approximately on surfaces of uniform thermosteric anomaly (δ_T). Salinity is shown plotted on two surfaces of uniform δ_T that were chosen to lie within the layers of shallow maximum and minimum salinity (Fig. 5). The advantage of this presentation over others is that on surfaces of uniform δ_T the gradients of temperature and salinity exist solely because of water mass differences. On a surface of uniform depth these gradients are compounded by gradients that are a result of adjustment to baroclinic flow.

The shallow salinity maximum for TC72 closely follows the isanostere $\delta_T = 266$ cl t^{-1} ($\sigma_t = 25.32$) which lies mostly within a depth range of 90 to 170 meters. This surface, as is true of the other choice, lies deeper toward the south. The salinity on the surface where $\delta_T = 266$ has a greater range of values and larger gradients than at the sea surface (Fig. 5). The cores of high salinity project across the map as narrow tongues aligned with the geostrophic flow, as given by the field of acceleration potential (figure not shown but very similar to surface flow). The cores suggest swift and narrow jets of flow and counterflow, and thus demonstrate perhaps more clearly than geostrophy the character of the circulation. These narrow cores are often identified by the use of a single station along each section; thus, the resolution of these features is very limited. (The narrow band of salinity > 34.6‰ near 34°30′N (Fig. 5) is drawn dashed westward to 140°W based on a second occupation of this transect). The pattern of the salinity distribution on this surface is similar to that at the sea surface except that the features are enhanced. The largely subsurface core of high salinity projecting northeastwardly near 37°N is centered about this surface. The transition zone has a relative low in salinity (<34‰) projecting westward. The contours depicting each of these features is commensurate with the geostrophic flow.

The salinity minimum (TC72) that underlies the shallow maximum follows the isanostere $\delta_T = 220$ cl t^{-1} ($\sigma_t = 25.81$). This surface also falls within the subarctic halocline and extends below the subtropical halocline, lying mostly between 125 and 230 m. At $\delta_T = 220$ cl t^{-1}, the salinity gradients are considerably reduced and are shown contoured at an interval of 0.1‰ (Fig. 5). The same major features continue to be reflected in the salinity field at this level as above, including gradients at the location of the northern subtropical front.

5. The fronts in June 1974

The strong frontal regime observed in 1972 and 1973 was largely dissipated by June 1974 (Fig. 6). Each of

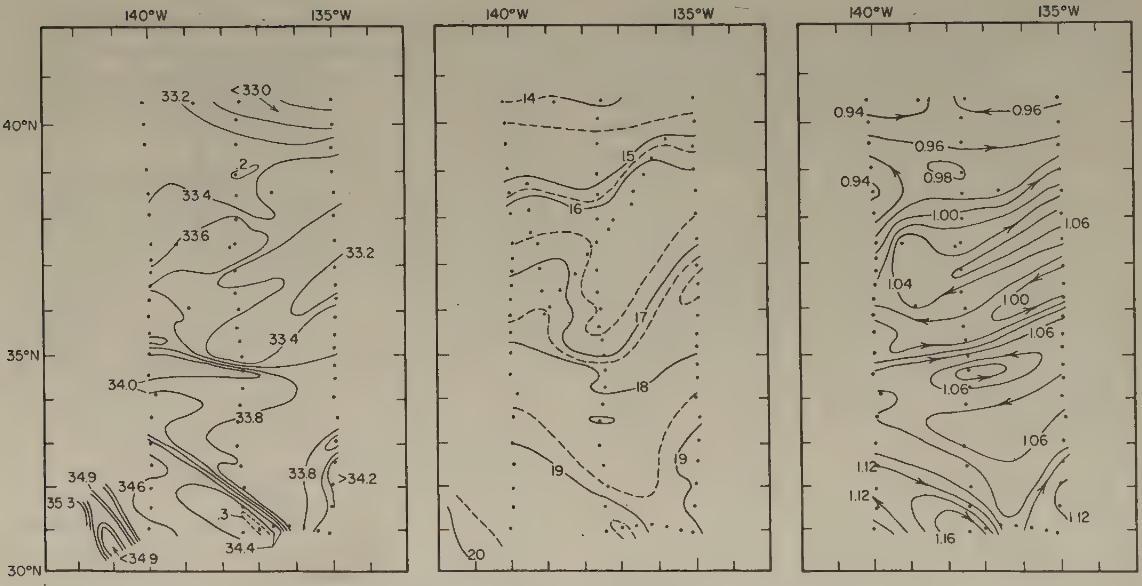

140°W
135°W
40°N
35°N
30°N
33.2
<33.0
2
33.4
33.6
33.2
33.4
34.0
33.8
34.9
34.6
35.3
33.8
>34.2
3
34.4
<34.9
14
15
16
17
18
19
19
20
0.94
0.96
0.96
0.94
0.98
1.00
1.06
1.04
1.00
1.06
1.06
1.06
1.12
1.12
1.16
1.12

FIG. 4. Data from TC72. Left, sea surface salinity (‰) derived from continuous recording salinograph; center, sea surface temperature (°C, station data only); right, geopotential anomaly at the sea surface relative to 500 db (dynamic meters or 10 $m^2 s^{-2}$).

the fronts has penetrated farther northward than was the case in the preceding years. This crossing of the subtropical front gives it a double character, at 31° and 31°30′N. The northern subtropical front is well-defined by the salinity gradients but it has a smaller range of salinity and slightly lesser values, 34.1–34.4‰, than earlier. The range of temperature at mid-depth is also reduced. The band of high salinity with the subsurface maximum (about station 31) is still evident but it is no longer situated against the northern subtropical

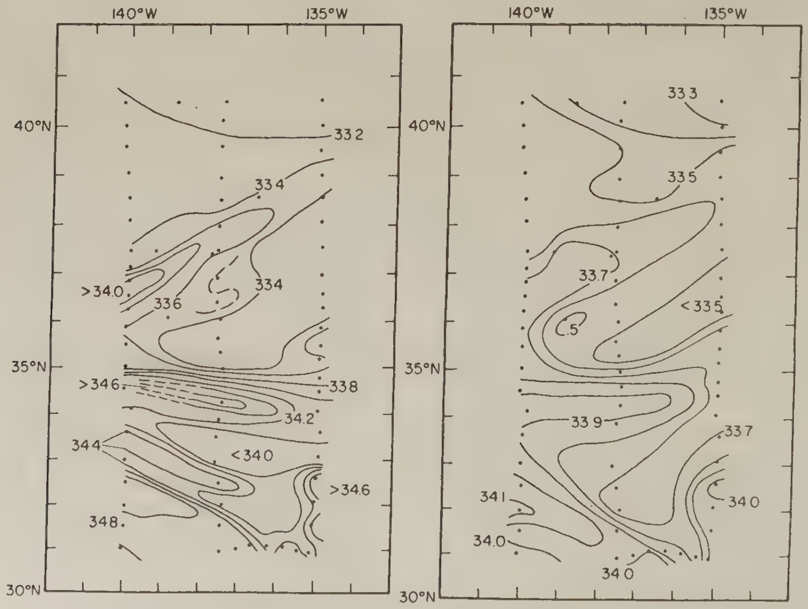

140°W
135°W
40°N
35°N
30°N
33.2
33.4
>34.0
33.6
33.4
>34.6
33.8
34.2
34.4
<34.0
>34.6
34.8
33.3
33.5
33.7
<33.5
.5
33.9
33.7
34.1
34.0
34.0
34.0

FIG. 5. Data from TC72. Left: salinity (‰) on the surface where $\delta_T = 266$ cl/ton; right: salinity on the surface where $\delta_T = 220$ cl/ton. Contour interval of salinity in the left panel is 0.2‰ and in the right panel, 0.1‰.

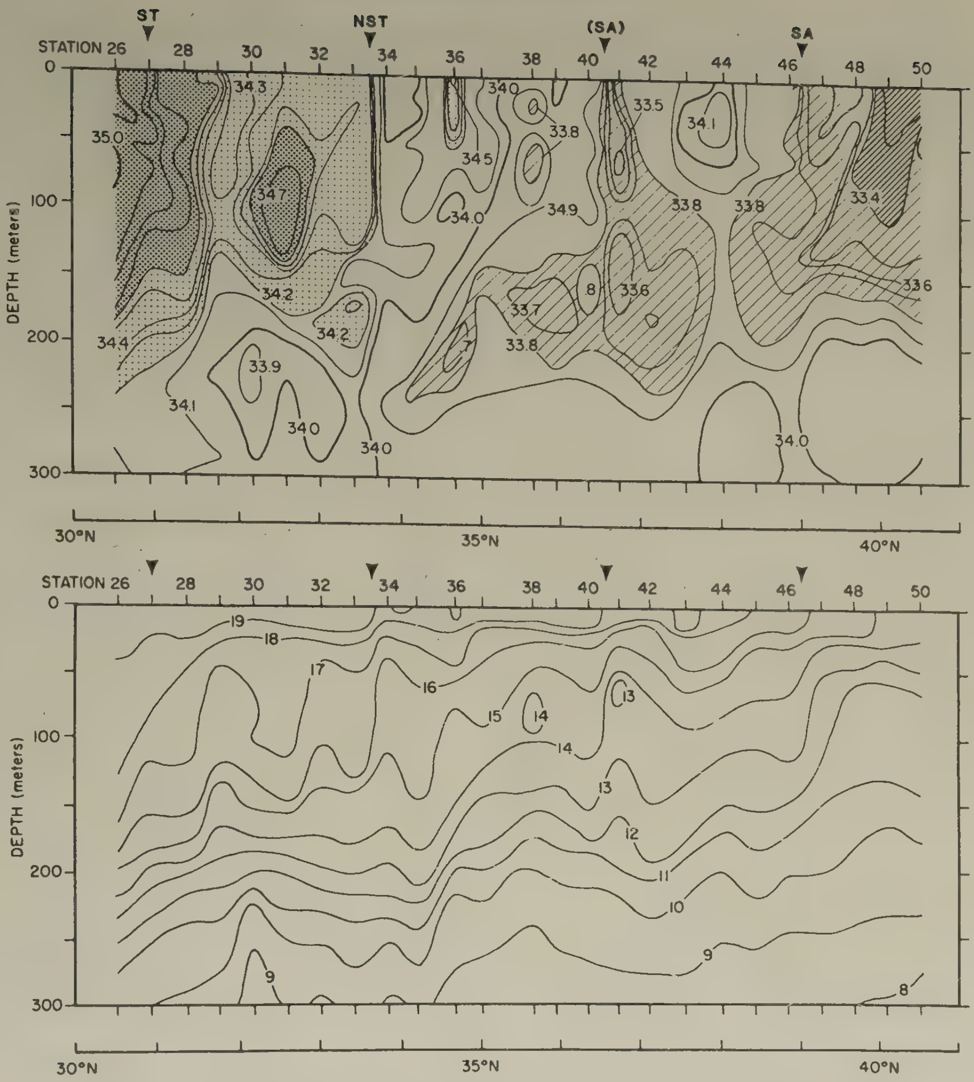


FIG. 6. Vertical sections of salinity and temperature along 137°30′W from cruise DSJ74 (June 1974). Station spacing is nominally 37 km.

front. The shallow salinity maximum within the transition zone is rudimentary (150 m, station 34). The largest differences from other years occur in the transition to subarctic waters. A weakened subarctic front is found at 39°N and a remnant of this front is found at 36°30′N. The range of temperature and salinity across this front is also reduced. At both manifestations of this front the shallow salinity minimum projects southward at about the level of the subarctic halocline. Additional shorter transects to the west and east of the 137°30′W transect (Fig. 1) confirm the foregoing description. Laurs and Lynn (1977) attribute a large difference in the behavior of albacore during the 1974 fishing operations conducted in cooperation with this survey to the poor development of the subarctic front. They noted that in 1972 and 1973, the albacore cued on or were indirectly influenced by the presence of these fronts during their springtime shoreward migration. In 1974 the corraling effect of a strong frontal regime was missing and the albacore spread rapidly throughout this region during June.

6. The fronts in June 1975

A single long transect of stations was taken in June 1975, from the Straits of San Juan de Fuca to off Hawaii

(Fig. 1). The three major fronts were clearly delineated in the distributions (not shown). The subarctic and northern subtropical fronts were found along 137°30′W at 36°20′N and 32°15′N, respectively. The subtropical front was found at 29°40′N, 138°20′W. The strength of frontal development resembled that for 1972 and 1973. Flow was strong and deep at the northern subtropical front. Eastward geostrophic velocity (relative to 1000 db) increased from 12 cm s^{-1} at the surface to 14 cm s^{-1} at 180 m, and remained above 10 cm s^{-1} to 340 m. Weak and westward flow was associated with a pocket of relatively lower-salinity water between the subtropical and northern subtropical fronts.

7. The fronts in June 1976

The 9-km station spacing used in observing the northern subtropical front during June 1976 provides a much improved resolution of the salinity and temperature structure (Fig. 7). In order to accommodate the higher resolution, the vertical sections in Fig. 7 and the remaining vertical sections for June 1976 are plotted at half the vertical exaggeration as was used in the previous figures. Salinity changes 0.8‰ in 36 km which matches most of the earlier findings. The band of high salinity along the southern wall of this front has values that exceed 34.8‰ and is very narrow. Salinities exceeding 34.7‰ at all levels within the band fall within a span of 18 km. There is a well-defined layer having a maximum in salinity that projects northward into the transition zone at 130 m. The northern subtropical front again lies near 32°N; thus, this position is common to four of the five years of observations.

The only westward geostrophic flow of significance in Fig. 7 (up to 14 cm s^{-1} calculated relative to 1000 db) occurs in the subtropical waters south of station 81. Eastward flow prevails from 60 km south of the northern subtropical front to 40 km north of it. The flow appears as bands having velocities of 20–35 cm s^{-1} interspersed with bands having negligible velocities. Geostrophic computations from such closely spaced stations are very sensitive to the resolution of the input measurements; i.e., distance between stations and the station-to-station difference in steric height. (For 9 km at this latitude, a difference of 2 dynamic cm in steric height gives 30 cm s^{-1}.) They are also affected by time variations in the density field, which are likely in such an energetic region. Stations 81–92 were completed in 21 hours, hence, less than 2 hours elapsed between any pair of stations for which velocities were calculated. The STD used had a history of a very steady calibration. Positions were determined with an OMEGA system by experienced navigators. Although reasonable estimates of errors in measured values could alter computed velocities by several centimeters per second or more, it would take compounding of multiple errors of unexpected magnitude to alter significantly the general pattern of velocity given in Fig. 7. The individual values of velocity may be subject to some error; however, it is evident that the characteristic bandedness in the flow about the fronts is difficult to dismiss. Neither is it unequivocally demonstrated, although the commonality of scale of salinity features and bands of flow is supportive.

Contours of surface salinity about the northern subtropical front based on the continuous record of the thermosalinograph also show its banded nature (Fig. 8). The filament of high salinity (>34.8‰) which lies to the south of the major gradient at 32°N is the surface manifestation of the prominent band of salinities extending to 150 m in Fig. 7. Unfortunately the ship's track did not cross the entire front to the west of 138°30′W; the salinity filament could not be identified there. However, a glancing pass into surface waters ex-

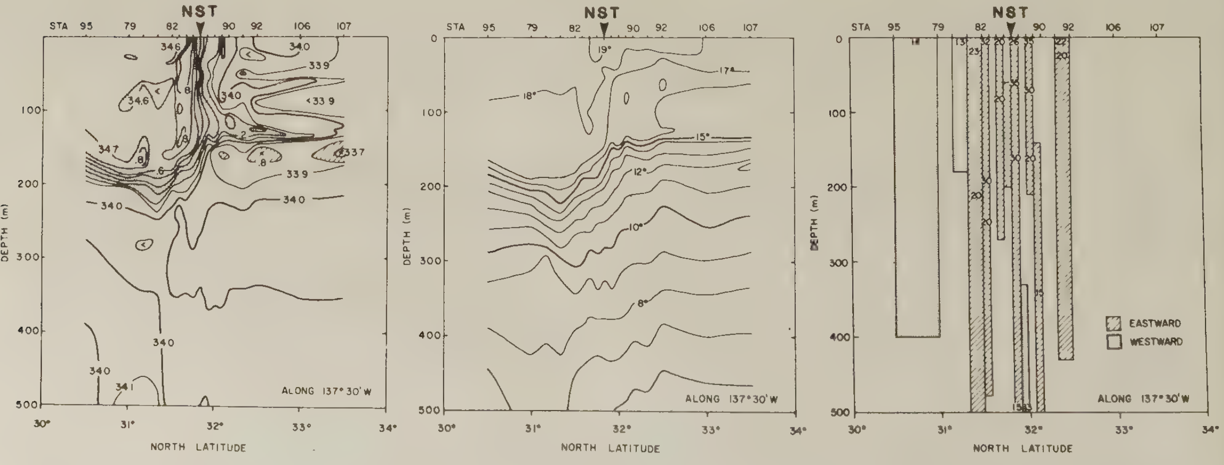


FIG. 7. Vertical sections of salinity, temperature and geostrophic velocity along 137°30′W for June 1976. Only the northern subtropical front is shown. Vertical exaggeration here and in Fig. 9 is 927, half of that used in previous figures. Station spacing is variable; at its least it is 9 km.

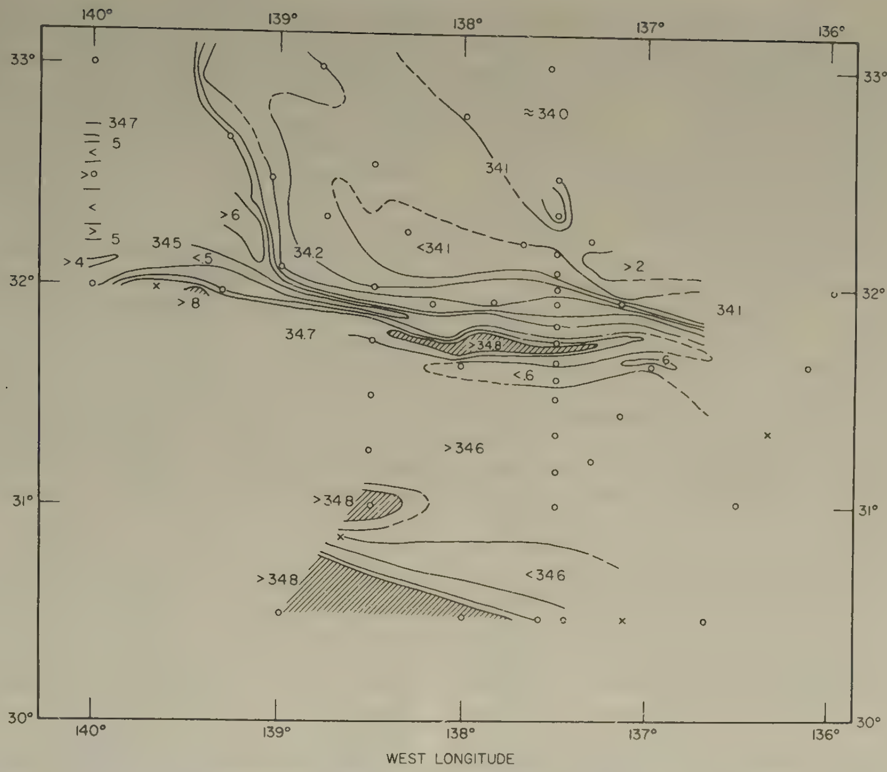


FIG. 8. Contours of surface salinity about the northern subtropical front derived from the thermosalinograph. The open circles and crosses are positions of STD and XBT casts, respectively.

ceeding 34.8‰ at 139°30′W indicates that this filament may extend over at least 250 km. The surface salinity trace of the easternmost line of stations (Fig. 8) taken on June 7 did not show the filament and neither did the first (northward) pass along 137°30′W on June 8. It was evident in frontal crossings after June 12 (and along 137°30′W on June 14). Thus, the surface appearance of the band is intermittent. As a subsurface feature it appears consistently in the 5-year data series. This is so despite the fact that its apparent width in 1976 shows that sometimes it could be aliased by the 36 to 54 km spacing between stations of the early surveys.

There are filaments of relative lows in Fig. 8, as well. One of these occurs immediately to the north of the front (<34.1‰) and another immediately to the south of the high-salinity filament (<34.6‰). This particular cross-frontal pattern was often seen in the surface salinity traces at both the northern subtropical and the subarctic fronts.

In 1976 the subarctic front, 34°30′N (Fig. 9), is farther south than in the observations of other years. In contrast to the comparatively large width, 500 km, of the transition zone in 1975, it was the narrowest, 250 km, in 1976. The vertical sections of Fig. 9 are for a transect near 138°30′W, set orthogonal to the front (aligned along 105°T). The 9-km station spacing used across the subarctic front greatly improves the resolution of the gradients. The front is well-developed and the features characteristic of the front are all in evidence. Eastward geostrophic velocities reach 25 cm s^{-1} between 30 and 70 m for the station pair (137–138) between which the largest lateral salinity gradient is found. Eastward flow prevails at stations immediately to the south of these stations, as well. On the low-salinity side of the frontal gradient the flow is westward, reaching 16 cm s^{-1}. The largest lateral shear appears to coincide with the front.

8. Comparison with Saur's data

Saur (1980) discussed aspects of the fronts and the transition zone in a study of surface temperature and salinity observations taken in a 9-year time series (repeated approximately every 2 or 3 weeks) along a great-circle route between Honolulu and San Francisco. This route crosses the survey region of the present study and is shown in Fig. 1. The period of the time series, 1966–70 and 1972–75, encompasses that of the surveys described herein with the exception of the last one. His

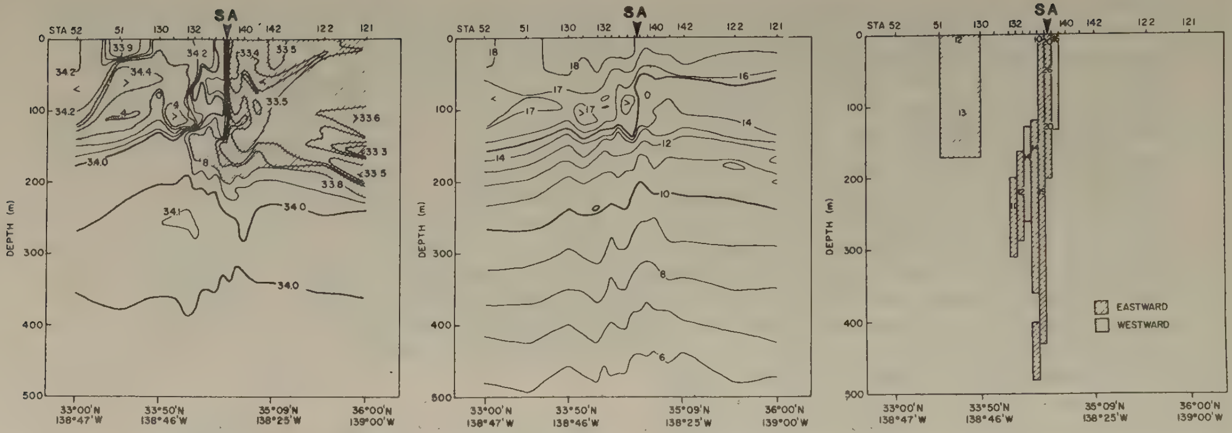


FIG. 9. Vertical sections of salinity, temperature and geostrophic velocity for a transect perpendicular to the subarctic frontal gradients: stations 132–142, spaced at 9 km, are aligned along 13°T and across 138.5°W. Additional nearby stations at larger intervals complete the figure.

study examines the temporal development and dissipation of fronts. The large distances between observations (usually 120 or 165 km) provide only a gross estimate of the surface gradients at any one time; however, this record produces temporally coherent patterns.

Saur finds the fronts to have been strongly developed during the latter part of 1972 and through the summer of 1973. Beginning in late 1973 the gradients weakened, and through 1974 the frontal pattern was confused although some continuity existed in the gradient that he identified as the subtropical front. By spring 1975 a stronger frontal system had reformed. The vertical sections presented herein match these events very well. Based primarily upon the positive correlation of temperature and salinity anomalies, Saur speculates that these changes, which are a part of longer term events, are primarily related to the variation in strength of circulation about the eastern limb of the subtropical gyre. Stronger-than-normal circulation produces negative temperature and salinity anomalies such as during the fall–winter of 1972/73. It also increases the magnitude of the surface gradients. The opposite occurs when the circulation is weaker than normal.

Saur finds that the salinity gradients migrate at a velocity of about 1.5–2.3 cm s^{-1} along the great-circle route to the southwest in the manner of annually forced baroclinic waves. They appear at the outer edge of the low-salinity California Current waters, and eventually dissipate in the high-salinity waters of the subtropics.

The detailed observations of this new series may offer some clues to the events revealed in the temporal surface records. There is evidence of mesoscale meanders that stretch zonally in which the stronger gradients are subsurface. The saline intrusion at 37°N depicted in Fig. 5 is a prominent case. If this feature grew and broke through to the surface (and downward through the halocline) it would produce a new manifestation of the subarctic front at a more northeastwardly position. The waters pinched off to the south would eventually mix to form the waters of intermediate characteristics found in the transition zone. Similar events might involve the two subtropical fronts to form the subsurface saline cores. If these features are peculiar to these longitudes, it may be that they are related to circumstances that are regional. The most obvious circumstance is the reorientation of the fronts from a zonal path to one that is southeasterly following the eastern limb of the large subtropical gyre.

9. Discussion and conclusions

The comparison of these observations, repeated each June for five years, reveals some idea of the variability in frontal development as well as the opposite—those aspects which appear to recur each year. Although Saur's analysis of biweekly observations of surface temperature and salinity supports the year-to-year differences seen in the vertical sections, it is clear that there are occurrences of spatial differences in frontal structure that are as large or larger than some of the annual differences. The estimation of temporal variability cannot be carried much beyond the generalities presented. The interesting finding is that in each of the five years the fronts are readily identifiable by a set of characteristics in every crossing and show well developed horizontal gradients in most of them. Some of these vertical sections, mostly constrained as they were to meridians, may have made oblique crossings to the meandering fronts. However, in every observation there are strong horizontal gradients of salinity, coincident with horizontal gradients of temperature, each front has its own range of salinity and temperature, and each has a definite association to halocline structure. There are complex features in the salinity distribution that are part of the frontal zone structure. These include layers, bands and cores of extremes. The shallow salinity minimum that projects southward from the base of the subarctic front has been described as a product of wind-driven Ekman convergence, sinking along the northern edge of the subarctic front in winter and spreading at depth because of a differing orientation of baroclinic flow at depth from that near the surface (Niiler and Reynolds, 1984). The shallow salinity maximum, most prominent where it projects northward from the northern subtropical front, has an appearance that suggests a similar generational source but neither the wind field nor the flow field is known to an adequate resolution to test this idea.

The association of geostrophic velocity with the fronts is seen to be quite variable in this dataset. There are instances when flow at the front appears to be negligible. However, for the most part, flow is stronger and extends deeper close about the fronts than elsewhere. Its variability may be greater about the subarctic front. In addition to the findings reported here, strong eastward flow directly associated with the subarctic front was found during a survey conducted aboard the R.V. *David Starr Jordan* in July 1971 (unpublished data). This front, found at 35°20′N, 135°W was well developed. In a crossing perpendicular to the front, having ten stations spaced at 9 km, there was a 28 km-wide band of eastward flow in excess of 10 cm s^{-1} (referencing 1000 db) that encompassed the entire horizontal gradient. The flow reached 42 cm s^{-1} on the high-salinity side of the front.

The bands and cores of salinity extremes show a close association with the geostrophic flow pattern. Because geostrophic velocity is computed for a pair of stations, and the extreme value of salinity within the core is described by a single station, the correspondence of the velocity field and such a feature may at times be ambiguous. However, an examination of the multiple occurrence of high-salinity cores shows that they are flowing eastward. In fact, all features that have locally high salinity are in regions of predominantly eastward flow. The westward flowing waters tend to be local low-salinity regions. An example of the latter event occurs between the subtropical front and the northern subtropical front.

There is an association of the vertical distribution of velocity and salinity. Where there is a subsurface core of high salinity or a subsurface northward protrusion of subtropical waters, there is a marked likelihood for a subsurface maximum velocity (eastward) to occur at or near the same level. The typical increase in subsurface velocity over the surface value is on the order of 1–2 cm s^{-1}.

The determination of velocity across fronts and about associated complex salinity structure by the method of geostrophic computation has obvious flaws. Among them are inadequate spatial resolution and poor adherence to the assumption of steady state. Despite these flaws the repetition of observations, taken as a whole, provides a reasonable description of the gross circulation and its effect upon the water mass structure. The fields of velocity, salinity and temperature suggest a confluence of flow toward the frontal zones. It is particularly evident that the eastward flowing band of high-salinity water on the southern side of the northern subtropical front must have its source to the south and west. The larger patterns in this circulation, such as large eddies, are not resolved in these data. The surveys do not encompass the source of cores and bands of salinity extremes.

This series of surveys reveals the existence of the northern subtropical front as a quasi-permanent feature. The repetition, year-to-year, of the particular ranges of temperature and salinity characteristics at the northern subtropical front, the differences of the ranges from those of the subtropical front and the simultaneous observations of both the subtropical front and this additional front show these fronts to be separate structures. The differences in ranges of characteristics and the physical separation are the same as seen in Roden's (1980) observations of two zonal fronts between 155 and 151°W.

There are additional published data that support the hypothesis that the northern subtropical front is a major feature over a large extent of the North Pacific like its counterparts to the north and south. A front observed at 30°30′N, 133°W (Roden, 1974) has the same characteristics. This front lies along a path described by the mean distribution of surface layer salinity (Robinson, 1976). The 133°W meridian nearly marks the easternmost extent of the waters that characterize the subtropical front. It lies near 27°30′N.

In the western North Pacific the ranges of temperature and salinity characteristics of the Kuroshio Extension front (Kawaii, 1972; Masuzawa, 1972) include those found at the northern subtropical front. The Kuroshio Extension front lies along the axis of the Kuroshio Extension Current which meanders between 33° and 36°N (Kawaii, 1972; Roden, 1982), a latitudinal range which includes the northern subtropical front (west of 150°W). The subtropical front in the western North Pacific is found at latitudes between 25°N to 30°N (White, Hasunuma, and Solomon, 1978).

In its path eastward, the Kuroshio Extension encounters large bathymetric features, the Shatsky Rise (163°E) and the Emperor Seamount Chain (170°W), which affect its course and diminish its strength (Roden et al., 1982; Levine and White, 1983). Roden et al. (1982) find that to the east of the seamounts the Kuroshio Extension current widens three-fold and appears to be poorly defined there. Maps of the modulus of horizontal temperature gradient at the 300-m level reveal multiple branchings of the Kuroshio Extension Current system about the major bathymetric features (Levine and White, 1983). Of the resulting downstream bands of thermal gradient one continues eastward along a zone about 35°N to the vicinity of 165°W where the horizontal thermal gradient at 300 m weakens below their defining limits. Levine and White labeled this the Kuroshio Extension front. In the eastern North Pacific the water-mass frontal structure is above 150 m and the baroclinicity is weaker than in the west. Hence, the modulus of temperature gradient at 300 m does not provide the means to reveal its eastward extent beyond 165°W.

Observations that address the zonal continuity of the thermohaline frontal structure of the Kuroshio Extension east of the seamounts are vertical sections of temperature and salinity along meridians 178° and 158°W, Figs. 1 and 2 of Roden (1970). These sections, drawn from closely spaced CTD casts for April, show frontal structure above 150 m at 36°N, 178°W and at 34°N, 158°W. Both features involve the same isolines of temperature and salinity as those characterizing the Kuroshio Extension and northern subtropical fronts. Taken as a whole, this body of evidence shows that the underlying thermohaline structure of the northern subtropical front has its genesis in the Kuroshio Extension current and, although largely weakened about the Emperor Seamount Chain, it is continuous or quasi-continuous across the North Pacific reaching as far east as 133°W. In various regions and during various periods these horizontal gradients are greatly enhanced by frontogenetic processes described by Roden (1980) and Niiler and Reynolds (1984).

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